JOURNAL OF AGRICULTURAL RESEARCH

VOL. 39 WASHINGTON, D. C., SEPTEMBER 1, 1929 No. 5

INFLUENCE OF VARIETAL RESISTANCE, SAP ACIDITY, AND CERTAIN ENVIRONMENTAL FACTORS ON THE OCCURRENCE OF LOOSE SMUT IN WHEAT[1]

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INTRODUCTION

During the 10-year period 1917–1926, for which records are available,[3] loose smut (*Ustilago tritici* (Pers.) Jens.) in the United States took an estimated toll of wheat which averaged more than 10,000,000 bushels annually. (Fig. 1.) Measures for controlling the disease in this country, however, rarely are applied. The very close association of the host and parasite throughout their life cycles makes practical control a difficult matter. The modified hot-water treatment of the seed, which has been generally recommended during the last 20 years and which has proved to be the best treatment yet devised, is effective in control. However, it involves a number of operations which make it tedious and difficult to apply under usual farm conditions.[4] Moreover, the treatment retards emergence of

[1] Received for publication Feb. 26, 1929; issued September, 1929. A thesis submitted to the faculty of the graduate school, Cornell University, in partial fulfillment of the requirements for the degree of doctor of philosophy, June, 1927. Results of varietal-resistance tests in 1927 and 1928 are not included in the thesis.

[2] The writer wishes to express his thanks to H. H. Whetzel, professor of plant pathology at Cornell University, for helpful suggestions; to H. H. Love, professor of plant breeding at Cornell University, for providing facilities for carrying out the experiments in 1924–25; and to C. E. Leighty, Office of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, for supplying most of the seed samples used in the experiments and for assistance in identifying varieties.

[3] UNITED STATES DEPARTMENT OF AGRICULTURE. BUREAU OF PLANT INDUSTRY. The following mimeographed material from Plant Disease Bulletin (or Reporter):

ESTIMATE OF CROP LOSSES DUE TO PLANT DISEASES. 1917. Plant Disease Bul. 2(1), 18 p. 1918.
CROP LOSSES FROM PLANT DISEASES. 1918. Sup. 6, p. 186–213. 1919.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1919. Sup. 12, p. 307–332. 1920.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1920. Sup. 18, p. 317-338. 1921.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1921. Sup. 24, p. 489–510. 1922.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1922. Plant Disease Rptr., Sup. 30, p. 462–490. 1923.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1923. Sup. 36, p. 318–348. 1924.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1924. Sup. 43, p. 381–410. 1925.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1925. Sup. 49, p. 382–412. 1926.
CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES IN 1926. Sup. 56, p. 394–423. 1927.

Also the following mimeographed supplements of the Plant Disease Bulletin (or Reporter):

FROMME, F. D. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1920. Sup. 15, p. 115–176, illus. 1921.
HASKELL, R. J. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1923. Sup. 35, p. 244–348, illus. 1924.
——— DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1925. Sup. 48, p. 301–381, illus. 1926.
——— DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1927. Sup. 62, p. 302–353. 1928.
———and WOOD, J. I. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1922. Sup. 27, p. 164–266, illus. 1923.
KIRBY, R. S., and ARCHER, W. A. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1926. Sup. 53, p. 110–208, illus. 1927.
MELCHERS, L. E. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1924. Sup. 40, p. 106–191, illus. 1925.
STAKMAN, E. C. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1921. Sup. 21, p. 139–254, illus. 1922.

[4] These operations are: A 4 to 6 hour presoaking of the seed in cold water, a momentary tempering dip at about 120° F., a 10-minute bath at about 129°, sowing of the treated seed in a separate plot, and, finally, separate harvesting of the plants from treated seed.

seedlings and generally reduces germination and yield (*34*, *35*).[5] The inconspicuous nature of the loss caused by loose smut in wheat doubtless also helps to account for the lack of an active practicing

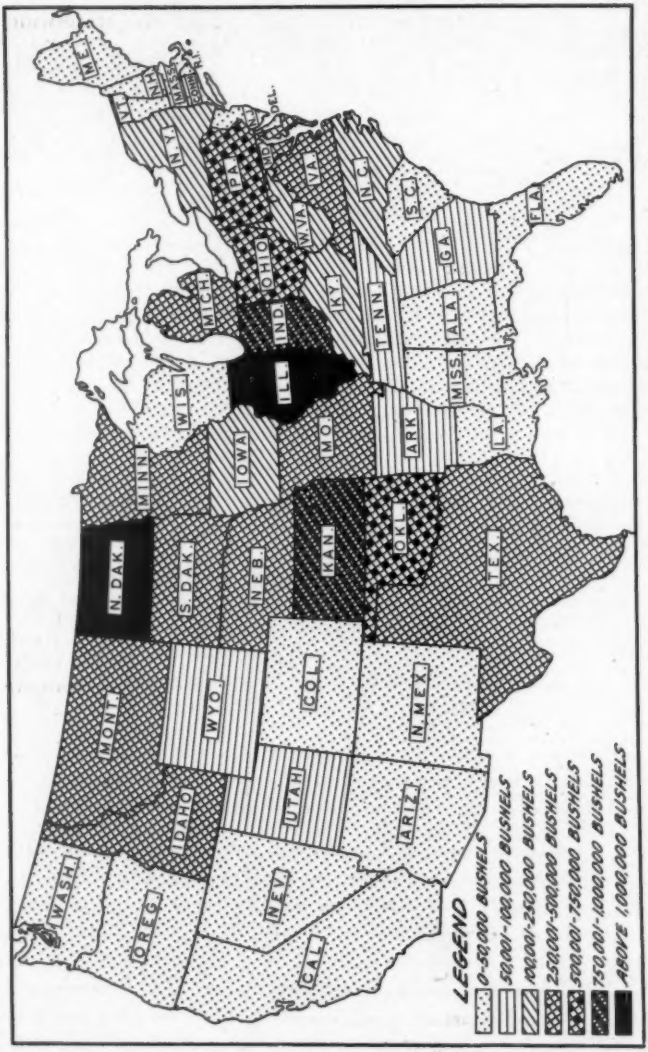

FIGURE 1.—Estimated average annual reduction of wheat production (bushels) due to loose smut in each State for the period 1917–1926, inclusive. The average reduction in bushels for each State has been placed in one of seven groups, as shown in the legend. Data compiled from estimates of the Plant Disease Bulletin (footnote 3)

of control. The smutted heads, the only signs of the disease that are readily apparent, are in evidence for a few days only, i. e., during the blooming period of the healthy heads. As a result, growers

[5] Reference is made by number (italic) to "Literature cited," p. 337.

frequently are led to underestimate or to overlook entirely the amount of grain destroyed and the need for control. Moreover, loose smut in wheat never becomes alarmingly severe except in individual fields or within limited territory. Five per cent of diseased heads seems to be the highest amount that has been recorded for state-wide areas.[6] It is difficult, therefore, to enlist a general interest in control among growers, especially in view of the fact that all the known control measures are relatively difficult of application.

In consideration of these factors it would seem that the control of loose smut in wheat presents a problem particularly adapted for solution through the selection or development of resistant varieties, or of resistant strains within varieties which are susceptible but nevertheless desirable. To this end the studies on varietal resistance reported herein were undertaken with a number of wheats mostly from the eastern half of the United States. There are reported herein also the results of studies to determine (1) a possible correlation between high acidity in the cell sap of wheat of different varieties and their resistance to loose smut, and (2) the extent to which certain environmental factors may influence the amount of disease exhibited by a particular variety. Several previous investigations, as noted later, indicate that some of these factors may influence the occurrence of loose smut in some wheats.

LIFE HISTORY OF THE CAUSAL ORGANISM

The causal fungus (*Ustilago tritici*) hibernates as mycelium within the wheat seed, vegetates systemically, and fruits in the young wheat heads previous to their emergence, destroying most of the tissues of the spike, except the rachis (fig. 2), and producing a black powdery mass of smut spores in their stead. The infested kernels and the plants developed from them show no external evidence of the presence of the pathogene previous to the emergence of the smutted heads. Smutted and healthy heads emerge during approximately the same period, and spores from the former are disseminated through the air while the healthy heads are in bloom. (Fig. 2.) Inoculation is intraseminal, being effected by the chance falling of one or more errant spores on the ovary or stigma which is exposed through opening of the glumes in the process of blooming. Leighty and Sando (*25*) found that the time required for a wheat flower to open fully in blooming averaged 3 minutes and 36 seconds, while the time from beginning of opening to complete closing averaged 26 minutes and 30 seconds. It is evident, therefore, that the exposure of the flower to possible infection is of short duration. Moreover, the infection count is small. These facts doubtless explain why, as previously noted, epiphytotics of loose smut do not occur. Within a few days all the spores are blown or washed from the diseased heads, and only the naked rachises of the spikes persist. (Fig. 3.) Following its inclusion within the glumes the spore soon germinates with the protrusion of a germ tube which eventually enters the developing kernel wherein the mycelium is developed. The mycelium finally hibernates within the matured kernel, and the life cycle is thus completed.

[6] United States Department of Agriculture. Bureau of Plant Industry. Op. cit.

FIGURE 2.—A, Healthy blooming head of wheat; B, smutted head. Healthy heads are in flower and spores are blown from diseased heads during approximately the same periods. Inoculation is effected by the falling of a spore upon the stigma or the ovary during the brief period of their exposure at blooming when the flowering glumes usually open for a few minutes and the anthers are extruded

The difficulty of controlling loose smut in wheat through seed treatment becomes readily apparent in view of the fact that the smut fungus is carried inside the seed. Surface disinfectants which control stinking smut and other surface-borne smuts have proved ineffective. Treatments which thoroughly soak the seed, like the modified hot-water treatment, are necessary to kill the intraseminal mycelium of the loose-smut fungus.

REVIEW OF PREVIOUS INVESTIGATIONS ON THE CONTROL OF LOOSE SMUT IN WHEAT

A review of the literature shows that a number of different methods have been tried for controlling loose smut in wheat, namely, (1) the selection of large kernels; (2) the use of seed more than 1 year old; (3) the removal of smutted plants from the field; (4) the use of clean seed; (5) the treatment of the seed with chemicals, hot water, hot air, and steam, alone or in some combination; and (6) the selection of resistant strains and varieties. A full review of the effectiveness of these different methods was given by Appel and Riehm (*2*) in 1911. Since that time further studies of the methods have been made (*3*, *4*, *8*, *17*, *27*, *29*, *32*, *34*, *35*).[6] As a result of these investigations it has been found that, except for the use of varieties and strains which are resistant and otherwise desirable, treatment of the seed with hot

[6] UNITED STATES DEPARTMENT OF AGRICULTURE. BUREAU OF PLANT INDUSTRY. Op. cit.

water is the best method of control in general farm practice. Hot water may be applied in different ways (*17*, *35*). The modified method devised by Freeman and Johnson (*10*) has been generally recommended during the past 20 years. This treatment, as noted previously, is practiced only to a limited extent. It is effective in control but relatively complicated and tedious to apply in comparison with other standard cereal-seed treatments. The other methods of control enumerated above, except the use of resistant varieties, have been found either impracticable of application or ineffective in control or both.

With regard to the use of resistant varieties and strains, the literature apparently fails to show that any specific tests have been made to determine through floral inoculation the resistance or susceptibility of the more important varieties grown in the United States. Differences in susceptibility exhibited by specific classes or varieties of wheat have been observed, however, by a number of investigators. Kellerman and Swingle (*22*) note that loose smut is said to attack summer wheats most, winter wheats less, and hard wheats and spelt least of all. According to Melchers[7] also, the hard wheats in Kansas have less smut than the soft wheats. Freeman and Stakman (*11*) observed that durum wheats seem to have comparatively little loose smut, but of the common Minnesota spring wheats the bearded varieties seem to have more than the bluestems and fifes; however, no common variety showed any marked resistance to the disease. Fromme (*13*) also has reported that bearded wheats show uniformly more loose smut than the beardless varieties. In one case observed by him the average amount of loose smut in 20 bearded varieties was almost three times that found in 16 beardless varieties.

In specific varieties of wheat the occurrence of loose smut or its absence has been noted by Arthur (*5*), Kellerman (*21*), Maddox (*28*), Coons and Spragg (*9*), Fromme (*13*, *14*), Tieman (*36*), various contributors to the Plant

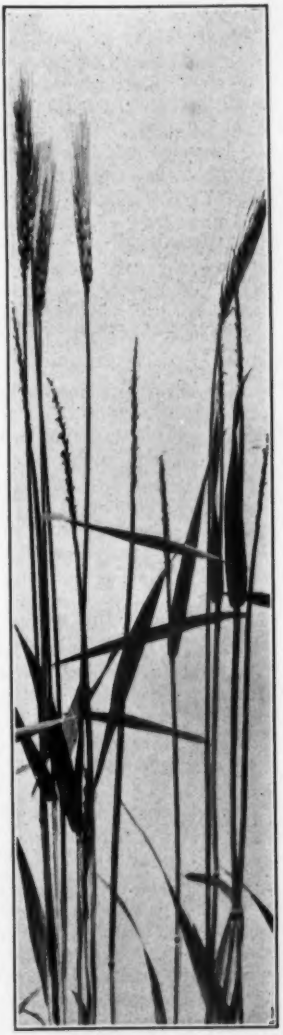

FIGURE 3.—Healthy heads of wheat at the close of the flowering period, and diseased heads from which the smut spores have been blown or washed, leaving only the naked rachis of the spikes

[7] MELCHERS, L. E. Op. cit. (See footnote 3.)

Disease Reporter,[8] and others. The content of loose smut in the varieties observed has been reported in various ways, and an accurate summary of the data would be difficult to present. A number of varieties have been reported resistant by some and susceptible by others. It is evident, however, that only a very few varieties have been consistently reported as showing any marked degree of resistance.

Several experiments have been recorded briefly with regard to the selection of resistant strains in susceptible varieties. Strube (*33*) isolated a strain of Red Schlanstedt spring wheat which was said to be both highly resistant to loose smut and superior in yield and strength of stem. Recently Fromme (*14*) reported the results of susceptibility tests with a number of strains of Fulcaster wheat. Some have been found to be twenty times as resistant as the parent, indicating the probability of developing a highly resistant strain of this important variety.

INFECTION STUDIES

A COMPARATIVE STUDY OF THE ANTHESIS OF RESISTANT AND SUSCEPTIBLE WHEATS

It has been suggested (*13*) that apparent resistance in varieties may be due simply to escape of disease by virtue of a relatively cleistogamous habit of blooming, to an anthesis of shorter duration, or to both. If this were true, then in the artificial insertion of inoculum the effectiveness of this weapon of the plants' defense, as it were, would fail to receive due consideration. Appel (*1*) stated that immunity from loose smut in certain types of barley is due to closed flowers, and Brefeld and Falck (*6*) obtained abundant infection by the introduction of spores into the artificially opened flowers of a cleistogamous variety of barley in which loose smut never had been observed. In wheat, cleistogamy does not occur, except under certain environmental conditions unfavorable for the opening of the glumes, as noted by Leighty and Sando (*25*).

Detailed studies on the duration and degree of glume opening in the anthesis of resistant and susceptible wheats apparently have not been made. Fromme (*13*) noted that in a cursory examination he failed to find any differences that appeared to be significant in the blooming of the resistant Leap and the susceptible Stoner varieties. Both were observed to open during pollination.

During the period June 1–6, 1925, the writer made a comparative study of the anthesis of 25 flowers of Dawson (C. I.[9] 6161) and an equal number of Forward (C. I. 6691) wheat. The two varieties were grown at Ithaca, N. Y., under similar conditions, and in adjacent rows 1 foot apart. Dawson is a beardless soft winter wheat with brown glabrous glumes and white kernels. It has been consistently reported very susceptible to loose smut.[6] The plants used in this study were grown from seed from hand-inoculated flowers and contained 27.08 per cent of smutted heads. Forward also is a beardless soft winter wheat but with white glabrous glumes and red kernels. Recent surveys indicate that it may not be so highly resistant as

[8] United States Department of Agriculture. Bureau of Plant Industry. Op. cit.

[6] United States Department of Agriculture. Bureau of Plant Industry. Op. cit. (See footnote 3.)

[9] Numbers preceded by C. I. are accession numbers of the Office of Cereal Crops and Diseases.

reported earlier,[6] but there seems to be no doubt that it is far more resistant than Dawson. The Forward plants used in this experiment also were grown from seed from hand-inoculated flowers. No smutted heads appeared. Observations of the anthesis were made between 7 and 9 a. m. Both the duration and the degree of opening of the glumes were measured. The latter measurement was obtained by superimposing the points of a pair of dividers over the tips of the lemma and palea at the time of blooming when the filaments were completing their elongation and the anthers were assuming a pendent position. The divider points then were pressed into a sheet of paper, and later the distance between the two imprints was measured carefully. The distance averaged 3 mm. for both varieties. The time from the beginning of opening to complete closing was approximately 26 minutes for both varieties. Near the completion of anthesis the glumes close very slowly, and it was therefore difficult to determine the precise moment at which the process was completed. In view of these facts, it is apparent that resistance to loose smut in Forward is not a function of the mechanics of anthesis. The writer had observed also that the Leap variety, for example, which in the field consistently bears a very low percentage of loose smut,[6] continues to do so when the flowers are inoculated artificially. (Table 2.) Moreover, if the mode of anthesis was the factor upon which resistance depended, then there should be expected no significant differences in the percentages of infected plants and heads displayed by different varieties when inoculated artificially. Reference to Table 2 shows, however, that the assembled varieties, grown and inoculated by hand under similar conditions, consistently displayed wide differences in percentages of smutted heads.

It may be noted here that the date of blooming of a variety in a particular locality apparently may enable it to escape loose smut. In the very early variety Nebraska No. 28 (C. I. 5147), for example, high percentages of smutted heads and plants were obtained in the hand-inoculation tests. (Table 2.) On the other hand, loose smut has not been observed in the fortieth-acre plots of this variety at the Arlington Experiment Farm, near Washington, D. C. It seems that this is due to the fact that blooming in this variety occurs before the air has become laden with inoculum from smutted heads in the plots of later varieties. Doubtless a very late habit of blooming also would enable a susceptible variety to escape disease under normal conditions, provided that the seed sown was clean.

EFFECT OF STAGE OF ANTHESIS ON INFECTION BY USTILAGO TRITICI

According to Freeman and Johnson (*10*), "artificial inoculations of flowers with loose smut from the time when the stamens are still green to the time when the ovary is one-third its mature size are usually successful. The optimum period for artificial inoculation is at the time when the flower is in full bloom or when the ovary is just commencing to develop after fertilization." In experiments conducted by the writer, however, inoculation succeeded best when the inoculum was inserted while the pollen was still immature. This is shown in Table 1.

[6] UNITED STATES DEPARTMENT OF AGRICULTURE. BUREAU OF PLANT INDUSTRY. Op. cit.

TABLE 1.—*Effect of stage of anthesis on the infection of Stoner[a] and Red Chaff[a] wheats by Ustilago tritici*

Wheat variety	Stage of anthesis at inoculation	Year plants were grown	Number of seeds sown	Plants matured		Plants smutted		Heads		
				Number	Per cent	Number	Per cent	Total number	Number smutted	Per cent smutted
Stoner	Pollen green	1923	50	35	70.0	25	71.4	303	81	26.7
Do	Pollen being shed, or a few hours thereafter.	1923	100	40	40.0	4	10.0	299	15	5.0
Red Chaff	Pollen green	1924	200	99	49.5	76	76.8	885	514	58.1
Do	Pollen being shed, or a few hours thereafter.	1924	200	108	54.0	60	55.6	1,053	444	42.2

[a] According to Clark, Martin, and Ball (7), Stoner is a synonym for Fulcaster, and Red Chaff is a synonym for Goens wheat.

In the method employed by Freeman and Johnson (*10*), all the flowers on a head were inoculated, the stage of anthesis being designated as the average of all the flowers on the head. In the writer's method only those flowers on each head which were in the stage designated were inoculated. All others were removed in order to delimit the designated stage of anthesis as closely as possible. To this difference in method the difference in results obtained by Freeman and Johnson (*10*), and by the writer may be attributed, although varietal differences and other factors also may have had some influence.

In the studies which follow, as noted previously, flowers with green pollen were not inoculated. It may be noted, however, that Hussar (C. I. 4843), Leap (C. I. 4823), Purplestraw (C. I. 1915), and several other varieties which have proved to be highly resistant to loose smut invariably have continued to remain so even when inoculated while the pollen was still green.

VARIETAL RESISTANCE AND SUSCEPTIBILITY

METHODS

The ideal method of inoculation would consist in placing one or several spores of *Ustilago tritici* on the exposed ovary or stigma of a wheat flower in full bloom. This method is hardly practicable, however, because the individual flowers on a spike are wide open for only a few minutes while the duration of blooming on a head may extend from two to seven days (*23*, *25*). After some experimentation with different methods of artificial inoculation, a modification of one of the methods of Brefeld and Falck (*6*) was found most satisfactory and was adopted for all the inoculation studies reported herein except where otherwise noted. It consisted in opening the flower, when necessary, and lightly touching the stigma with the tips of forceps that had been dipped in a mass of smut spores. By this method the opening and inoculation of the flower were accomplished in one operation, and after some experience it was possible to attain considerable speed. This was a vital point to consider in view of the large number

of flowers to be inoculated during the short period in which blooming occurs. In 1923, 1924, and 1925 spores were taken from single smutted heads selected at random as needed from different plots. In 1926 and 1927 a large number of smutted heads from different plots were first collected, then the smut was taken from the heads and sifted through a fine screen. The composite sample thus obtained was used for inoculating the different varieties. The sifted smut was placed in a small capsule held in a clamp fastened to a ring. The device, ordinarily used for carrying pollen, is described by Leighty and Sando (*26*).

Inoculations were made on flowers which were (1) open, (2) on the verge of opening, or (3) had opened shortly before. To this end there were selected heads which contained in the lower two-thirds of the upper half of the head a relatively large number of flowers which were open or which had opened shortly before, as indicated by the unbleached extruded anther sacs and the still plumose condition of the stigma. As the flowers in this portion of the head are the first to open (*25*), the heads so selected therefore also contained in the adjacent upper and lower portions of the head a relatively large number of flowers on the verge of opening, as indicated by the color of the pollen sacs in the particular variety at hand. Many of these flowers on the verge of opening were stimulated to open as a result of handling the head in the process of inoculation. Freeman and Johnson (*10*) have shown that the period during which wheat flowers are susceptible to infection extends from a time when the pollen is still immature until the fertilized ovary has attained approximately one-third of its mature size. In the method here employed, therefore, the inoculations were made during a period which fell well within the limits of possible infection. All flowers not inoculated were removed. As a rule only the two lower flowers in a spikelet were inoculated and the upper flower or flowers were removed. At the distal portions of the heads a few entire spikelets generally were detached. Flowers were inoculated on plants grown both in the field and in the greenhouse, but most of the inoculations were made in the field. This is shown in Table 2. Each inoculated head was tagged, harvested at maturity, and threshed in a small machine especially constructed so that every kernel was recovered.

The seed was sown by hand. Individual kernels were spaced 6 inches apart in rows 1 foot apart when sown in the field, or 2 inches apart in rows 6 inches apart when sown in the greenhouse. Through this method of spacing the seed the full complement of heads of each of the individual plants always was easy to recognize. Most of the sowings, as noted in Table 2, were made in the field. The crop of 1925 was grown at Ithaca, N. Y., and previous and later crops were grown at the Arlington Experiment Farm, Rosslyn, Va. The wheats were sown in autumn during the usual sowing period at these places. All of the sowings were made with seed from the preceding crop.

In the selection of varieties for inoculation particular attention was paid to the soft red winter common wheats. Varieties in this group are most extensively grown in the middle States east of the Mississippi (*24*) where loose smut is most prevalent[6] and usually are suitable for

[6] UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. Op. cit.

growth in the environment of Rosslyn, Va., or Ithaca, N. Y., where the tests were conducted.

For some varieties listed in Table 2, the total number of plants and heads on which the data are based is relatively small because only a small percentage of the plants matured. This was due in large measure to the following facts: (1) The plants were widely spaced, and hence matured later; (2) infected seedlings proved more susceptible to winter killing (p. 333); and (3) some of the varieties were not very well adapted to the environmental conditions of one or the other of the localities where grown.

The appearance of approximately 6 to 10 per cent or more of loose-smutted heads in a variety was arbitrarily selected as a basis for considering it susceptible and discontinuing it in the test. It was not possible to establish an inflexible basis in this regard, as the inoculation of a variety could not be delayed always until the last of the diseased heads had appeared. In a few cases a variety was temporarily discontinued because it had passed the stage suitable for inoculation during a period when time was not available for inoculating all the wheats in bloom.

MATERIALS

Most of the varieties used in these studies came from the collection assembled for the study of wheat classification by members of the Office of Cereal Crops and Diseases (7). Many of the varieties were grown from seed selected from individual heads in previous seasons and thus were pure-line selections, whereas others represent merely the mass variety, as indicated in Table 2. It may be possible, therefore, that other pure lines of these varieties would show more or less loose smut. In some of the more important varieties several strains have been tested, so that the behavior of the variety, as a whole, is fairly well indicated.

RESULTS OF VARIETAL TESTS

The data obtained in the varietal resistance and susceptibility tests are presented in Table 2. The recognized varieties are listed in alphabetical order following the nomenclature used by Clark, Martin, and Ball (7). All synonymous names of varieties are listed together in alphabetical order or in the order of their Cereal Investigations (C. I.) numbers under the recognized varietal names. The varieties tested belonged to one of the three groups—common, club, or durum. The common wheats included varieties in each of four commercial classes (hard red spring, hard red winter, soft red winter, and white wheats).

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculated flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*

[Wheats grown at Arlington Experiment Farm, Rosslyn, Va., in 1923, 1924, 1925, 1927, and 1928, and at Ithaca, N. Y., in 1925. Except when the year is followed by a footnote reference, the flowers were inoculated on plants growing in the field and the seeds which developed were sown in the field]

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Alton:								
Ghirka Winter	1438	Pure line	Hard red winter common.	1924	59	69.49	514	47.66
Backa:								
Wisconsin Pedigree No. 408.	6156	do	do	1926			1,002	2.30
Do	6156	do	do	1927	55	0	145	0
Beloglina:								
Beloglina	1667	do	do	1926			856	8.76
Big Frame:								
Big Frame	6184	do	Soft red winter common.	1926			576	5.73
Blackhull:								
Blackhull	6251	Mass selection	Hard red winter common.	1925	11	0	124	0
Do	6251	do	do	1926			292	0
Do	6251	do	do	1927	6	0	18	0
Brown Fife:								
Brown Fife	1933	do	Soft red winter common.	1923	69	57.97	572	22.02
Buffum No. 17:								
Buffum No. 17	3330	Pure line	do	1926			134	8.21
China:								
China	180	Mass selection	do	1923	75	54.66	585	23.41
Pennsylvania Bluestem.	4816	Pure line	do	1924	41	78.04	451	34.58
Climax:								
K. B. No. 2	4835	do	do	1926			556	6.83
Currell:								
Currell's Prolific	3326	Mass selection	do	1923	82	63.41	598	31.60
Golden Chaff	5578	Pure line	do	[a] 1924	18	33.33	100	4.37
Do	5578	do	do	1925	25	4.00	148	1.35
Do	5578	do	do	1926			426	11.97
Dawson:								
Dawson Golden Chaff.	—	Mass selection	White common	1925	48	27.08	358	12.57
Do	3342	Pure line	do	[a] 1924	85	0	669	0
Do	3342	do	do	1925	25	0	132	0
Do	3342	do	do	1926		0	57	0
Do	3342	do	do	[b] 1926		0	49	0
Do	3342	do	do	1927	63	23.81	384	11.20
Do	3342	do	do	1928	64	95.32	651	36.10
Do	3342	do	do	[b] 1928	97	85.57	97	85.57
Honor	6161	Mass selection	do	1923	67	44.77	525	16.00
Democrat:								
Democrat	3384	Pure line	do	1924	63	47.61	731	21.06
Diamond Grit:								
Diamond Grit	3385	do	Soft red winter common.	1924	23	47.82	231	23.27
Diehl-Mediterranean:								
Diehl-Mediterranean.	1395	do	do	1923			521	5.76
Do	1395	do	do	1927	61	72.13	130	50.77
Eaton:								
Eaton	4682	do	White common	1925	2	50.00	5	20.00
Eureka:								
Eureka	5170	Mass selection	Hard red winter common.	1925	112	66.07	908	30.18
Evans:								
Evans	2946	do	Soft red winter common.	1923	64	0	387	0
Do	2946	do	do	1924	50	20.00	345	16.52
Flint:								
Flint	6612	do	do	1924	97	46.39	522	33.90

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the field, and the seed which developed was sown in the greenhouse.

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculated flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*—Continued

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Forward:								
Forward	6691	Mass selection	Soft red winter common.	1923	61	0	351	0
Do	6691	do	do	1924	22	0	106	0
Do	6691	do	do	1925	64	0	489	0
Fulcaster:								
Bearded Purple-straw.	1911	do	do	1923	37	0	218	0
Do	1911	do	do	1924	57	26.31	369	6.23
Dietz Longberry	1981	do	do	1923	40	2.50	306	1.96
Do	1981	do	do	1924	37	43.24	193	15.54
Fulcaster	—	do	do	1925	50	8.00	362	1.10
Do	6162	do	do	1923	37	18.91	212	23.58
Marvelous	3605	do	do	1923	49	0	272	0
Do	3605	do	do	1924	46	2.17	269	1.11
Do	3605	do	do	1925	26	0	117	0
Stoner	2980	do	do	1923	75	38.66	602	15.94
Fultz:								
Fultz	1923	do	do	1923	54	37.03	412	15.53
Do	3416	Pure line	do	[a] 1924	82	0	893	0
Do	3416	do	do	1925	54	0	388	0
Do	3416	do	do	1926			458	1.53
Do	3416	do	do	1927	202	37.13	842	18.29
Fultzo-Mediterranean:								
Fultzo-Mediterranean.	5813	Mass selection	do	1923	87	25.28	621	14.33
Genesee Giant:								
Early Genesee Giant.	1744	Pure line	White common	1925	56	35.71	206	17.96
Gipsy:								
Defiance	5305	do	Soft red winter common.	1925	78	0	560	0
Gipsy	—	do	do	1925	44	0	516	0
Do	—	do	do	1926		0	528	0
Do	—	do	do	1927	257	6.23	831	2.17
Do	—	do	do	1928	39	61.54	392	17.85
Do	3439	Mass selection	do	1923	87	1.14	611	.15
Do	3439	do	do	1924	80	30.00	563	10.47
Gladden:								
Gladden	5577	do	do	1923	79	7.59	715	4.47
Do	5577	do	do	1924	70	20.00	423	8.51
Goens:								
Goens	3428	do	do	[b] 1923	6	100.00	23	95.65
Red Chaff	—	do	do	1924	207	57.00	1,940	49.38
Goldcoin:								
Goldcoin	—	do	White common	1925	98	23.47	671	6.86
Junior No. 6	6971	do	do	1925	139	26.62	1,014	8.38
Golden Cross:								
Golden Cross	—	do	Soft red winter common.	1925	80	37.50	536	8.96
Grandprize:								
St. Louis Grand-prize.	4876	Pure line	do	1924	44	47.72	258	33.72
Harvest Queen:								
Harvest Queen	—	do	do	[a] 1928	35	77.15	404	66.84
Do	—	do	do	[b] 1928	34	76.47	34	76.47
Do	5314	do	do	1925	56	0	405	0
Red Cross	4882	Mass selection	do	1923	53	0	332	0
Do	4882	do	do	1924	90	1.11	465	.21
Do	4882	do	do	1925	59	11.86	418	7.89
Do	4882	Pure line	do	[a] 1924	115	.86	1,092	.09
Do	4882	do	do	1925	98	1.02	809	1.24
Haynes Bluestem:								
Haynes Bluestem	2874	Mass selection	Hard red spring common.	1923	71	33.80	515	20.38
Humpback:								
Humpback	3690	Pure line	do	1924	90	30.00	186	16.66

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the field, and the seed which developed was sown in the greenhouse.

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculated flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*—Continued

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Hussar:								
Red Hussar	4843	Pure line	Hard red winter common.	[a] 1924	179	0	662	0
Do	4843	do	do	[a] 1925	220	.45	1,102	.64
Hybrid 128:								
Hybrid 128	4229	do	Club	[a] 1924	163	93.25	528	89.58
Illini Chief:								
Illini Chief	5406	do	Soft red winter common.	1923	69	27.53	513	16.76
Imperial Amber:								
Imperial Amber	5338	do	do	1924	68	63.23	492	40.04
Jenkin:								
Jenkin Club	5177	do	Club	[a] 1924	138	97.10	463	97.62
Jones Fife:								
Jones Fife	4468	do	Soft red winter common.	[a] 1924	134	44.77	390	30.32
Kanred:								
Kanred	5146	do	Hard red winter common.	1925	62	3.23	464	.65
Do	5146	do	do	1926			535	5.23
Do	5146	do	do	1927	65	0	166	0
Kinney:								
Kinney	5189	do	Hard red spring common.	[a] 1924	24	75.00	279	68.10
Kota:								
Kota	5878	do	do	[a] 1924	90	95.55	487	93.42
Leap:								
Leap's Prolific	4823	do	Soft red winter common.	[a] 1924	112	0	926	0
Do	4823	do	do	1925	62	6.45	352	1.42
Do	4823	do	do	1928	62	9.67	595	2.69
Link:								
Missing Link	4866	do	White common	1926			314	12.74
Little Club:								
Little Club	4066	do	Club	[a] 1924	160	97.50	651	97.08
Lofthouse:								
Lofthouse	3275	do	Soft red winter common.	1926			60	3.33
Do	3275	do	do	1927	151	17.88	727	5.50
Longberry No. 1:								
Jones Longberry	3451	Mass selection	White common	1925	57	40.35	227	25.55
Mammoth Amber:								
Mammoth Amber	3355	Pure line	do	1926			467	16.70
Mammoth Red:								
Mammoth Red	2008	Mass selection	Soft red winter common.	1923	29	0	182	0
Do	2008	do	do	1924	66	18.18	390	7.43
Marquis:								
Marquis	3641	Pure line	Hard red spring common.	[a] 1924	149	23.48	458	17.68
Martin:								
Martin	4463	do	White common	[a] 1924	105	68.57	292	67.80
Mealy:								
Mealy	3358	do	Soft red winter common.	1924	67	4.47	661	.81
Do	3563	Mass selection	do	1923	38	0	267	0
Do	3563	do	do	1924	91	21.97	594	11.61
Mediterranean:								
Missouri Bluestem	1912	do	do	1923	71	0	622	0
Do	1912	do	do	1924	78	29.48	681	11.89
Rocky Mountain	1930	do	do	1923	65	24.61	759	7.24
Minhardi:								
Minhardi	5149	Pure line	do	1926			578	18.17
Minturki:								
Minturki	6155	do	Hard red winter common.	1926			928	6.90

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the greenhouse.

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculated flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*—Continued

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Nebraska No. 28:								
Nebraska Hybrid	5147	Mass selection	Soft red winter common.	1923	73	57.53	543	45.48
Nigger:								
Nigger	5689	do	do	1923	82	41.46	855	21.52
Nittany (Pa. No. 44):								
Nittany	6882	Mass selection	do	1923	72	0	398	0
Do	6882	do	do	1924	34	8.82	227	6.60
Do	6882	do	do	1925	51	0	259	0
Do	6882	Pure line	do	1925	64	18.75	538	8.18
O. A. C.:								
O. A. C. No. 104	6983	do	White common	1925	64	87.50	476	52.52
Oatka Chief:								
Oatka Chief	3481	Pure line	do	1926			480	14.17
Odessa:								
Odessa	6027	do	Soft red winter common.	[a] 1924	29	31.03	289	19.03
Do	6027	do	do	1924	81	9.87	800	8.00
Ontario Wonder:								
Ontario Wonder	3483	do	do	1926			356	19.10
Penquite:								
Velvet Chaff	5948	do	do	1924	98	0	681	0
Do	5948	do	do	1925	51	0	320	0
Do	5948	do	do	1926			235	0
Do	5948	do	do	1927	353	80.74	2,541	39.16
Do	5948	do	do	1928	71	88.74	744	37.91
Do	5948	do	do	[b] 1928	95	84.21	152	86.18
Pentad:								
Pentad (D–5)	3322	do	Durum	[c] 1924	8	0	6	0
Do	3322	do	do	[c] 1925	98	1.02	225	.41
Pesterboden:								
Weissenburg	1563	do	Hard red winter common.	1924	57	68.42	706	28.18
Peterson:								
Lars Peterson	5538	do	Soft red winter common.	[a] 1924	27	70.37	196	25.00
Poole:								
Poole	3488	do	do	[a] 1924	106	.94	1,227	.08
Do	3488	do	do	1924	31	3.22	215	1.86
Do	3488	do	do	1925	54	0	239	0
Do	3488	do	do	1926			398	6.78
Power:								
Power's Fife	3697	Mass selection	Hard red spring common.	1923	19	31.57	105	24.76
Do	3697	Pure line	do	[a] 1924	63	61.90	600	44.33
Prelude:								
Wisconsin Wonder	4323	Mass selection	do	[c] 1925	286	46.85	1,032	31.88
Preston:								
Preston	3328	Pure line	do	1924	72	4.16	715	1.53
Velvet Chaff	3081	do	do	[c] 1924	90	3.33	311	1.60
Do	3081	do	do	[c] 1925	140	.71	555	.36
Prohibition:								
Prohibition	4068	do	White common	1925	22	22.73	103	11.65
Prosperity:								
American Bronze	5380	do	Soft red winter common.	[a] 1924	48	52.08	335	16.41
Purplestraw:								
Purplestraw	1915	Mass selection	do	1923	27	0	176	0
Do	1915	do	do	1924	56	5.35	426	1.40
Do	1915	do	do	1925	54	3.70	265	.75
Do	1957	do	do	1923	19	0	119	0
Do	1957	do	do	1924	42	2.38	302	.99
Do	1957	do	do	1925	39	28.21	218	11.47
Red Chief:								
Early Red Chief	3392	Pure Line	do	1924	32	21.87	233	7.29

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the field, and the seed which developed was sown in the greenhouse.

[c] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the greenhouse.

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculated flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*—Continued

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Red Clawson:								
Early Red Clawson	5349	Mass selection	Soft red winter common	1923	69	15.94	552	6.34
Do	5349	do	do	1924	96	12.50	466	4.07
Red May:								
Beechwood	4886	Pure line	do	[a] 1924	33	39.39	375	14.40
Early Ripe	5319	Mass selection	do	1923	79	55.69	620	22.09
Jones Longberry	5339	Pure line	do	1925	39	74.36	287	40.42
Michigan Amber	4864	Mass selection	do	1923	70	64.28	486	22.22
Michigan Wonder	—	Pure line	do	1928	42	59.53	520	23.85
Do	—	do	do	[b] 1928	58	55.17	83	42.17
Red May	5336	Mass selection	do	1923	75	14.66	505	4.75
Do	5336	do	do	1924	21	9.52	123	3.25
Do	5336	do	do	1925	27	33.33	168	6.55
Red Rock:								
Red Rock	5976	do	do	1923	23	73.91	206	23.78
Do	5976	Pure line	do	1925	84	66.67	722	24.10
Red Russian:								
Red Russian	4509	do	do	[a] 1924	8	0	44	0
Do	4509	do	do	1925	26	11.54	147	5.44
Do	4509	do	do	1926	----	----	48	10.42
Red Wave:								
Red Wave	—	Mass selection	do	1925	102	74.51	626	37.06
Do	5804	do	do	1923	35	45.71	145	24.13
Rice:								
Rice	5734	Pure line	do	[a] 1924	39	5.12	287	3.83
Do	5734	do	do	1924	71	9.85	523	7.45
Ridit:								
Smutproof	6703	do	Hard red winter common.	[c] 1924	118	0	496	0
Do	6703	do	do	[c] 1925	183	0	947	0
Rudy:								
Rudy	5656	Mass selection	Soft red winter common.	1923	73	53.42	668	14.97
Rupert:								
Rupert's Giant	5920	Pure line	do	[a] 1924	106	66.03	778	21.20
Rural New Yorker No. 6:								
Red Hussar	3496	do	do	[a] 1924	33	39.39	267	11.23
Rural New Yorker No. 57:								
Rural New Yorker No. 57	3516	do	do	1926	----	----	850	27.17
Russian:								
Russian	5737	do	do	1924	71	23.94	617	4.37
Do	5737	do	do	1925	80	16.25	617	4.54
Do	5737	do	do	1926	----	----	1,020	1.47
Do	5737	do	do	1927	270	7.77	1,415	2.69
Seneca Chief:								
Seneca Chief	3575	do	White common	1924	39	69.23	392	15.81
Shepherd:								
Shepherd	6163	do	Soft red winter common.	1924	20	5.00	196	.51
Do	6163	do	do	1925	30	0	225	0
Do	6163	do	do	1926	----	----	377	0
Do	6163	do	do	1927	300	42.33	1,968	14.99
Sibley:								
Sibley New Golden	5666	do	do	1924	40	5.00	445	1.57
Do	5666	do	do	1925	34	5.88	255	2.35
Do	5666	do	do	1926	----	----	295	3.39
Do	5666	do	do	1927	152	21.05	717	10.74
Silvercoin:								
Silvercoin	6013	do	White common	1924	44	61.36	304	17.76
Silversheaf:								
Jones Silver Sheaf Longberry.	2496	do	Soft red winter common.	1924	32	3.12	259	.38
Do	2496	do	do	1925	37	0	212	0
Do	2496	do	do	1926	----	----	94	0
Do	2496	do	do	1927	333	47.15	1,990	18.49

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the field, and the seed which developed was sown in the greenhouse.

[c] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the greenhouse.

TABLE 2.—*Classified list of common, club, and durum wheats grown from seed from hand-inoculaed flowers, showing number of plants and heads and percentages of loose-smutted plants and heads*—Continued

Variety and synonyms	C. I. No.	Pure line or mass selection	Classification	Year in which plants were grown	Total plants	Plants smutted	Total heads	Heads smutted
					Number	*Per cent*	*Number*	*Per cent*
Sol:								
Sol	6009	Pure line	Soft red winter common.	1926			663	0
Do	6009	do	do	1927	277	0	735	0
Treadwell:								
Treadwell	5332	do	White common	1926			733	29.74
Trumbull:								
Trumbull	5657	do	Soft red winter common.	[a] 1924	34	0	448	0
Do	5657	do	do	1925	1	0	1	0
Turkey:								
Red Russian	3497	Mass selection	Hard red winter common.	1923	68	83.82	477	44.22
Theiss	1561	do	do	1923	52	0	212	0
Do	1561	do	do	1924	80	31.25	352	15.05
Turkey	1558	Pure line	do	[c] 1924	174	54.02	775	46.45
Do	6152	Mass selection	do	1923	72	47.22	824	7.03
Wheedling:								
Wheedling	4846	Pure line	Soft red winter common.	1924	64	31.25	633	6.31
White Fife:								
White Fife	4412	do	White common	1924	54	55.55	341	17.88
White Odessa:								
White Odessa	4651	do	do	[b] 1924	131	29.00	353	16.99
White Winter:								
White Winter	5219	do	do	1925	29	3.45	160	1.88
Do	5219	do	do	1926			583	.01
Do	5219	do	do	1927	60	30.00	109	11.93
Windsor:								
Extra Early Windsor.	5915	do	do	1925	73	52.05	389	24.16
Winter Bluestem:								
Winter Bluestem	5409	do	do	1926			84	21.43
Wyandotte:								
Wyandotte Red	3549	do	Soft red winter common.	[b] 1924	19	0	176	0
Do	3549	do	do	1925	14	14.29	83	4.82
Zimmerman:								
Zimmerman	2907	do	do	1924	45	31.11	254	26.77

[a] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the field.

[b] The flowers were inoculated on plants growing in the field, and the seed which developed was sown in the greenhouse.

[c] The flowers were inoculated on plants growing in the greenhouse, and the seed which developed was sown in the greenhouse.

Table 2 shows that Pentad (C. I. 3322), the only durum wheat tested, was highly resistant to loose smut. The three club wheats included in the test, Hybrid 128 (C. I. 4229), Jenkin (C. I. 5177), and Little Club (C. I. 4066), were strikingly susceptible, the latter two producing over 97 per cent of smutted plants and heads. (Fig. 4.) This is noteworthy in view of the fact that these wheats produce little or no loose smut in the Pacific Coast States, where they are grown extensively. It is probable that the extreme dryness of the atmosphere at infection time, i. e., when the wheats are in bloom, plays an important rôle in this connection. That higher humidities are favorable for infection is indicated by the fact that loose smut in these States is found in irrigated sections and also by the unusually high content of loose smut in the plants grown from seed from flowers inoculated under the humid conditions of the greenhouse. According to Tisdale et al. (*37*), the selections of Hybrid 128, Jenkin, and Little Club, noted above, as well as other selections, proved very susceptible to bunt also.

FIGURE 4.—Hybrid 128 (C. I. 4229), a club wheat grown from infected seed in a greenhouse at Arlington Experiment Farm, Rosslyn, Va. It produced 93.25 per cent of smutted plants, 89.58 per cent of smutted heads and many badly smutted leaves. The other club wheats included in the varietal test, Jenkin (C. I. 5177), and Little Club (C. I. 4066), produced over 97 per cent of smutted plants and heads. Many of the leaves also were badly smutted and distorted

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With regard to the common wheats, Table 2 shows that the range of resistance ran from almost complete susceptibility to immunity. Resistant and susceptible varieties were found within each of the four commercial groups, except that no resistant variety was found in the white wheats included in the test.

The varieties tested in each of the groups, which produced 5 per cent or less of smutted heads in each of the two or three years when grown, are listed in Table 3, and grouped in their respective commercial classes. Not included in the list are five varieties which produced less than 5 per cent smutted heads, but which have been tested in one year only. These varieties are: Fulcaster (C. I. —), Gipsy (C. I. 5305) Harvest Queen (C. I. 5314), and Mealy (C. I. 3358), soft red winter wheats; and Preston (C. I. 3328), a hard red spring wheat.

TABLE 3.—*Classified list of common wheats which produced 5 per cent or less of smutted heads in each of the years when grown from seed from hand-inoculated flowers at Rosslyn, Va., or Ithaca, N. Y.*

Variety and synonym	C. I. No.	Pure line or mass selection	Number of years tested	Total number of heads	Average percentage of smutted heads
HARD RED SPRING WHEATS					
Preston:					
Velvet Chaff	3081	Pure line	2	866	0.81
HARD RED WINTER WHEATS					
Bacska:					
Wisconsin Pedigree No. 408	6156	Pure line	2	1,147	2.01
Blackhull:					
Blackhull	6251	Mass selection	3	434	0
Hussar:					
Red Hussar	4843	Pure line	2	1,764	.40
Ridit:					
Smutproof	6703	do	2	1,443	0
SOFT RED WINTER WHEATS					
Forward:					
Forward	6691	Mass selection	3	946	0
Fulcaster:					
Marvelous	3605	do	3	658	.46
Leap:					
Leap's Prolific	4823	Pure line	3	1,873	1.12
Purplestraw:					
Purplestraw	1915	Mass selection	3	867	.92
Russian:					
Russian	5737	Pure line	3	3,669	2.94
Sol:					
Sol	6009	do	2	1,398	0
Trumbull:					
Trumbull	5657	do	2	449	0
Wyandotte:					
Wyandotte Red	3549	do	2	259	1.54

The occurrence of loose smut in many of the important wheats has been frequently reported in the Plant Disease Bulletins.[6] Examination of these reports shows that the varieties Blackhull, Forward, Leap, and Trumbull consistently have proved resistant in the States where grown. Reference to Table 2 shows that these varieties also

[6] UNITED STATES DEPARTMENT OF AGRICULTURE. BUREAU OF PLANT INDUSTRY. Op. cit.

were resistant when artificially inoculated. Likewise a number of varieties which have been uniformly reported highly susceptible also have proved highly susceptible in the varietal tests. Examples are: Currell, Dawson, Fulcaster (Stoner), Goens (Red Chaff), Kota, Red May (Michigan Amber), Red Wave, and Red Rock. (Tables 2 and 3.) Further examination of the data in the Plant Disease Bulletins[6] shows that certain varieties have been reported resistant in some localities and susceptible in others. Fulcaster, Fultz, Kanred, and Prelude (Wisconsin Wonder) are examples. These different findings may be due wholly or in part to a mixture of varieties, mistakes in identification of varieties, effects of different interactions of environmental factors in the various localities where the varieties were observed, particular strains of the causal organism with different powers of infection, particular strains of the wheat with different susceptibilities, or other causes. With regard to varieties with resistant and susceptible strains, reference to Table 2 shows that in Fulcaster, Gipsy, Harvest Queen, Mealy, Purplestraw, and Red May, some strains thus far have proved resistant while others are susceptible. Fromme (*14*) also has called attention to the existence in Fulcaster of races with different degrees of susceptibility. These findings lend encouragement to the possibility of reducing loose smut in the important susceptible wheats through the use of resistant pure-line selections.

The resistance of certain varieties in some localities and their susceptibility in others also may be due to the existence of physiologic forms of the causal fungus. Very recently Piekenbrock (*30*) has presented evidence to show that physiologic forms exist in the loose-smut fungus of wheat. In the course of the varietal tests the writer also has obtained evidence indicating their presence. For example, the varieties Fultz (C. I. 3416), Shepherd (C. I. 6163), Sibley (C. I. 5666), Silversheaf (C. I. 2496), and White Winter (C. I. 5219) were highly resistant or immune in 1926 and previously, but in 1927 they proved highly susceptible. Dawson (C. I. 3342), and Penquite (C. I. 5948) were immune in 1924, 1925, and 1926, but in 1927 and 1928 these pure-line selections proved highly susceptible. It is interesting to note, however, that Russian (C. I. 5737), highly resistant in 1924, 1925, and 1926, produced only 2.69 per cent of smutted heads in 1927. Flowers of Russian were inoculated in 1926 with the same composite smut sample used in the inoculation of the other wheats. The explanation of the sudden change in the reaction of the mentioned varieties in 1927 may be due to the fact that in 1923, 1924, and 1925 inoculum was taken from single heads, while in 1926 and 1927, as noted previously (p. 321), the inoculum was a composite sample of sifted smut from many different varieties. It seems probable, therefore, that one or more new and virulent forms may have been introduced in the sample, or a potent hybrid form may have been produced as a result of fusion of mycelia from different forms following inoculation.

The pure-line selections of Hussar (C. I. 4843) and Ridit (C. I. 6703) (Tables 2 and 3) used in the varietal test proved, respectively, highly resistant to and immune from loose smut. In experiments on the resistance of wheat varieties to stinking smut in the Pacific Coast States reported by Tisdale et al. (*37*), these same selections were used.

[6] United States Department of Agriculture. Bureau of Plant Industry. Op. cit.

Hussar was immune from stinking smut, and Ridit was highly resistant. These wheats, therefore, may prove valuable in breeding in sections of the country where both loose smut and stinking smut cause appreciable damage.

The results of the studies of resistance and susceptibility in the varieties shown in Table 2 may be summarized as follows: (1) Pentad, the only durum wheat tested, was highly resistant to loose smut; (2) the three club wheats tested (Hybrid 128, Jenkin, and Little Club) were highly susceptible, which is noteworthy in view of the fact that they produce little or no loose smut in the Pacific Coast States where they are grown extensively; (3) in the common wheats, the range of resistance extends from high susceptibility to apparent immunity; the highly resistant and immune varieties are relatively few, but one or more were found in each of the four commercial groups except the white wheats; (4) both resistant and susceptible strains were found in the important varieties Fulcaster, Gipsy, Harvest Queen, and Red May.

ACIDITY AND VARIETAL RESISTANCE OF WHEAT TO LOOSE SMUT

In recent years there has been considerable speculation regarding a possible interrelationship between resistance to disease and the concentration of hydrogen ions and titratable acid in the cell sap of the plant. Several varieties listed in Table 2 were grown from the same lots of seed used by Hurd in studies of acidity and varietal resistance of wheat to bunt, stem rust, and other diseases (*18*, *19*, *20*). The data, therefore, may be examined for possible correlations between resistance or susceptibility to loose smut and the corresponding acidity determinations reported by Hurd.

In studies of acidity with reference to stem rust, Hurd (*18*) found that the varieties Kota (C. I. 5878), Little Club (C. I. 4066), Pentad (C. I. 3322), and Preston (C. I. 3081) showed no evidence of significant differences in either hydrogen-ion or titratable-acid concentration at any stage of their development. In fact, the values were strikingly similar for varieties so unlike both in morphological type and susceptibility to stem rust (in general, Kota and Pentad are resistant and Little Club and Preston are susceptible). The resistance or relative susceptibility of each of these wheats to loose smut is shown in Table 4. As noted previously (Table 2), the varieties were pure-line selections. The plants were grown in the greenhouse from seed from hand-inoculated flowers.

TABLE 4.—*The resistance or susceptibility to loose smut shown by four wheats having cell sap with similar hydrogen-ion and titratable-acid concentrations*

Variety	C. I. No.	Classification	Year grown	Total number of plants	Number of plants smutted	Percentage of plants smutted	Heads		
							Total number	Number smutted	Percent smutted
Kota	5878	Hard red spring common.	1924	90	86	95.55	487	455	93.42
Little Club	4066	Club	1924	160	156	97.50	651	632	97.08
Pentad	3322	Durum	1924 1925	106	1	.94	271	1	.37
Preston	3081	Hard red spring common.	1924 1925	230	4	1.74	866	7	.81

Pentad and Preston are very resistant. Kota and Little Club are highly susceptible. It is evident, therefore, that no relation exists between the acid values of these varieties and their resistance or susceptibility to loose smut.

In studies of acidity of 1-week-old wheat seedlings and varieties variously resistant to bunt, Hurd-Karrer (*20*) again found no relation between either the hydrogen ion or the titratable acidity and resistance. She found that Hussar (C. I. 4843), Little Club (C. I. 4066), Ridit (C. I. 6703), and White Odessa (C. I. 4651) were characterized by a relatively high titratable acidity. The data in Table 2 show that Ridit is apparently immune to loose smut, Hussar is highly resistant, White Odessa is moderately resistant, and Little Club is extremely susceptible. Hurd-Karrer (*20*) also found that the varieties Hybrid 128 (C. I. 4229), Jenkin (C. I. 5177), and Jones Fife (C. I. 4468) were characterized by a relatively high hydrogen-ion concentration. Table 2 shows that Jones Fife is moderately susceptible and Hybrid 128 and Jenkin are highly susceptible to loose smut. The susceptibility of these varieties, and of Little Club with its relatively high titratable acidity, is further evidence that there is no causal relation between high acid concentration in the juice and ability to resist the invasion of *Ustilago tritici*.

PHYSIOLOGIC STUDIES

The foregoing results have shown that inherent differences in wheat varieties alone may be held accountable for differences in the percentage of loose-smutted plants and heads, and that these differences may range from 0 to almost 100 per cent.

That some environmental factors may have an important influence on the percentage of smuttedness within a variety also seems evident from the work of a number of investigators, as noted later, and from the experience of seed growers. With regard to the latter, the writer's attention frequently has been called to cases in which the variously distributed portions of a single lot of seed, sown at different times and on different soils, produced widely varying percentages of smutted heads. It has been the object of these studies, therefore, to ascertain the modus operandi of some of the factors and the possibility of decreasing loose smut in wheat through changes in agronomic practice which might reduce or completely control the disease.

INFLUENCE OF WINTERKILLING ON THE OCCURRENCE OF LOOSE SMUT

It has been noted by Coons and Spragg (*9*) in Michigan that infected wheat seems more likely to succumb to winterkilling than healthy wheat. In Virginia, Fromme [10] also has noted that infected seedlings seem less able to survive a severe winter. The relation between infection and susceptibility to winterkilling was studied by the writer in an experiment begun at the Arlington Experiment Farm, Rosslyn, Va., where the winters are relatively mild, and completed at Ithaca, N. Y., where the winters are relatively severe.

In the Virginia test, conducted in 1920–21, 72 different wheat lots representing 45 recognized varieties were used. Equal numbers of healthy and infected seed of each lot were sown in alternate rows. The number of seedlings which emerged before winter and the number

[10] FROMME, F. D. Op. cit. (See footnote 3.)

of plants which survived the winter and matured were recorded, as well as the percentage of smutted plants appearing in the latter. In the New York tests conducted in 1922–23 and 1924–25 a similar procedure was followed, but only a few varieties were used. The results in summarized form are presented in Table 5.

TABLE 5.—*Relative susceptibility of wheat seedlings from healthy and smut-infected seed to winterkilling when grown at Rosslyn, Va., and Ithaca, N. Y.*

Year	Location of experiment	Number of—		Condition of seed	Seeds sown	Germination	Seedlings before winter	Plants matured	Plants winterkilled		Smutted plants	Smutted heads
		Varieties	Lots									
						Per cent	*Number*	*Number*	*Number*	*Per cent*	*Per cent*	*Per cent*
1920–21	Rosslyn, Va.	45	72	Uninfected	1,857	76.36	1,418	1,300	118	8.32	0	0
				Infected	1,857	79.43	1,475	1,299	176	11.93	24.63	16.66
1922–23	Ithaca, N. Y.	3	3	Uninfected	230	89.57	206	147	59	28.64	0	0
				Infected	230	86.52	199	81	118	59.30	25.93	22.52
1924–25	do	2	2	Uninfected	800	57.13	457	344	113	24.73	0	0
				Infected	800	45.88	367	245	122	33.24	31.53	30.03

In each of the three years higher percentages of winterkilling occurred in plants grown from infected seed. In 1924–25 there was less winter injury to wheat in New York than usual, and the plants were grown in a sheltered area. For these reasons the 1922–23 results doubtless are more representative of the usual condition in New York.

At Ithaca, N. Y., fewer infected than uninfected seeds germinated, as shown in Table 5. Coons and Spragg (*9*) also obtained a poorer stand as well as more winterkilling of the susceptible "Goings" when grown from infected seed. This was not true when the resistant Shepherd's Perfection was so grown. It seems probable, therefore, that the natural checks on loose smut in susceptible varieties, particularly in districts having severe winters, are (1) a reduction in the number of seedlings which emerge from infected seed and (2) a higher percentage of winterkilling in the emerged seedlings from such seeds.

INFLUENCE OF VEGETATIVE VIGOR OF WHEAT IN RELATION TO RESISTANCE OR SUSCEPTIBILITY TO LOOSE SMUT

The work of Raines (*31*) and his review of many previous investigations show that increase in vegetative vigor of susceptible plants may be accompanied by increase or decrease in virulence of the disease, depending upon the particular plant and disease in question.

In a study of the effect of fertilizers on the susceptibility of barley to loose smut, Lind (*27*) found that the addition of Chile saltpeter, superphosphate, and potash, alone or in various combinations, increased the percentage of loose smut on six plots out of seven. In a series of plots sown to wheat continuously and receiving different quantities of fertilizers, Fromme (*12*) found more loose smut in plants grown on soils of low fertility than on soils of high fertility. Similar observations were made in connection with stinking smut in greenhouse plots. Heuser (*15*) and Hiltner and Lang (*16*) obtained similar results with bunt in field-grown plants, but the latter report that certain nitrogenous fertilizers appreciably increased both the vigor of

wheat plants and the percentages of loose smut which they produced. Tieman (*36*) found that fertilizers had very little influence on loose smut in wheat, except that phosphoric acid when used alone increased smuttedness.

The influence of the vegetative vigor of wheat on its resistance or susceptibility to loose smut was studied further by the writer in two experiments. The first was conducted in the greenhouse in 1922–23 and the second in the field the following year. In the greenhouse experiment, infected seed of Leap, a highly resistant wheat, and Goens (Red Chaff), a very susceptible wheat, was used. One hundred and twenty kernels of each variety were sown in a very rich soil, and a like number were sown in a very poor soil. The plants in the rich soil grew very vigorously, attained an average height of 35 inches, and produced an average of 4.87 heads per plant. The heads were large and well filled. On the other hand, plants on the poor soil grew very slowly, reached an average height of only 7 inches, and produced an average of only 1.11 heads per plant. The heads were small and poorly filled. It is evident, therefore, that the plants on the rich and the poor soils were extremely different in vegetative vigor. At maturity the height of the plants and the number of healthy and smutted plants and heads were recorded. The results are presented in Table 6.

TABLE 6.—*Influence of vegetative vigor on the occurrence of loose smut in Leap and Goens (Red Chaff) wheats grown in the greenhouse*

Variety	Kind of growth	Average height of plants (inches)	Average number heads per plant	Number of seeds sown	Number of plants matured	Percentage of plants matured	Number of plants smutted	Percentage of plants smutted	Total number of heads	Number of heads smutted	Percentage of heads smutted
Leap	Vigorous	35	5.29	120	86	71.67	8	9.30	455	23	5.05
	Weak	7	1.11	120	97	80.83	3	3.09	108	3	2.78
Goens	Vigorous	35	4.55	120	114	95.00	76	66.67	519	326	62.81
	Weak	7	1.12	120	113	94.17	72	63.72	126	78	61.90
Leap and Goens	Vigorous	35	4.87	240	200	83.33	84	42.00	974	349	35.83
	Weak	7	1.11	240	210	87.50	75	35.71	234	81	34.62

When growth of the plants was vigorous, higher percentages of smutted plants and heads were produced, especially by the Leap variety. However, the average percentage of smutted heads produced by vigorous plants of both wheats (35.83) was only slightly greater than that produced by weak plants of the two varieties (34.62).

The second experiment was conducted in 1923–24. The infected seed used in the resistance studies of that year was sown in the field in four successive plots numbered 1, 2, 3, and 4. Plots 1 and 4 were adapted for use in this special study. The procedure throughout the experiment was identical except that plot 4 received an application of manure at the rate of 20 loads per acre, and of phosphate at the rate of 200 pounds per acre, several weeks before the seed was sown. On each plot, 2,251 inoculated kernels, representing 70 different lots and 60 different varieties, were sown on October 26, 1923. In the following summer a record was made of the number of healthy and smutted heads on each of the plants which matured. A summary of the results is presented in Table 7.

TABLE 7.—*Influence of vegetative vigor on severity of loose smut in 70 different lots of wheat (60 varieties) when grown in the field on fertilized and unfertilized plots*

Item	Fertilized plot		Unfertilized plot	
	Number	Per cent	Number	Per cent
Seeds sown	2,251		2,251	
Plants matured	1,062	47.17	1,176	52.24
Heads	10,847		9,184	
Average heads per plant	10.21		7.81	
Infected plants	258	24.29	320	27.21
Infected heads	1,002	9.23	1,108	12.06

That the application of manure and phosphate induced a more vigorous growth is shown by the fact that plants on the fertilized plot produced an average of 2.4 more heads per plant than those on the unfertilized plot. Associated with this increase in vegetative vigor was a reduction in the percentage of smutted plants from 27.21 to 24.29 and in the percentage of smutted heads from 12.06 to 9.23.

The results obtained in the greenhouse and field experiments conducted by the writer, and those obtained by Fromme (*12*), Hiltner and Lang (*16*), and Tieman (*36*), show that the vegetative vigor of wheat grown from seed infected with the loose-smut fungus has little influence on its susceptibility and is without practical significance in control.

SUMMARY AND CONCLUSIONS

Loose smut of wheat takes an estimated toll in the United States of over 10,000,000 bushels annually. Measures for controlling the disease rarely are applied, however, due chiefly (1) to the endemic nature of the disease and its ready escape from observation, (2) to the relative impracticability of all the known control measures, including the generally recommended modified hot-water treatment, and (3) to the fact that the latter generally reduces germination, retards emergence, and decreases yield. In view of this situation, the problem of controlling loose smut of wheat seems especially suited for solution by selecting or breeding resistant strains or varieties.

The life history of the causal organism (*Ustilago tritici*) and the previous investigations on the control of loose smut in wheat are briefly reviewed.

A comparative study was made of the anthesis of the susceptible Dawson (C. I. 6161) and the resistant Forward (C. I. 6691) wheats to determine a possible relation to resistance. No relation was found, the extent and duration of glume opening being practically the same for both varieties. The varietal-resistance studies, in which inoculum was artificially inserted within the flowers, showed further that resistance was not due to escape from inoculum. Observations indicate that a very early or very late blooming may enable a variety to escape infection provided the variety itself is free from loose smut.

The stage of anthesis in which wheat flowers were inoculated was a factor in the susceptibility of the plants to infection. Inoculation while the pollen was still immature caused higher infections than those when the pollen was ripe, but the inoculation of several highly re-

sistant varieties when the pollen was immature did not affect their resistance.

In the varietal resistance and susceptibility studies, 102 recognized varieties and 132 different lots, mostly pure-line selections of eastern wheats, were tested from one to three years. The flowers were inoculated by hand.

Pentad (C. I. 3322), the only durum wheat included in the experiment, was highly resistant. The three club wheats tested, Hybrid 128 (C. I. 4229), Jenkin (C. I. 5177), and Little Club (C. I. 4066), were strikingly susceptible, the latter two containing over 97 per cent of smutted plants and heads. In view of the fact that loose smut occurs but rarely in the Pacific Coast States, where these wheats are mostly grown, it seems probable that the low atmospheric humidity which generally prevails there when the wheats are in bloom plays an important rôle in preventing their infection.

In the common wheats the range of resistance ran from high susceptibility to apparent immunity. The highly resistant varieties were relatively few, but one or more were found in each of the four commercial groups except the white wheats. Susceptible strains and strains which thus far have been resistant were found in the varieties Fulcaster, Gipsy, Harvest Queen, and Red May. The following 13 varieties have been tested for two or three years and have proved to be highly resistant or immune under the conditions of the experiment: Bacska (C. I. 6156), Blackhull (C. I. 6251), Forward (C. I. 6691), Fulcaster (C. I. 3605), Hussar (C. I. 4843), Leap (C. I. 4823), Preston (C. I. 3081), Purplestraw (C. I. 1915), Ridit (C. I. 6703), Russian (C. I. 5737), Sol (C. I. 6009), Trumbull (C. I. 5657), and Wyandotte (C. I. 3549).

The pure-line selections of Hussar (Red Hussar C. I. 4843) and Ridit (Smutproof C. I. 6703) were highly resistant to and immune from loose smut, respectively. These same selections also have proved highly resistant to stinking smut.

Evidence was obtained indicating the presence of physiologic forms in *Ustilago tritici*.

No correlation was found between the hydrogen-ion values or the titratable-acid values of the juice of wheat plants and their ability to resist the invasion of *Ustilago tritici*.

More winterkilling occurred in plants grown from infected seed than in plants from uninfected seed, at Rosslyn, Va., and at Ithaca, N. Y.

Wide differences in the vegetative vigor of wheat plants grown from seed infected with the loose-smut fungus had little influence on their susceptibility.

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RELATION OF LEAF ACIDITY TO VIGOR IN WHEAT GROWN AT DIFFERENT TEMPERATURES[1]

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INTRODUCTION

This investigation of the effect of temperature on leaf acidity was suggested by observations which indicated that any growth condition causing a decrease in the vegetative vigor of the wheat plant results in an increase in the acidity of its juice. For instance, winter wheats sown in the spring, which were so injured by unfavorable growth conditions that they failed to head, developed an abnormally high acid concentration (*8*).[2] These observations suggested that the acidity might vary consistently with the type of growth and so reflect the degree of adaptability of a variety to a given environment.

By growing both spring and winter varieties at each of three different temperatures, plants were obtained which differed greatly with respect to vigor and capacity for normal development. Comparative measurements of the acidity and moisture content of these plants at intervals during the growing period have given information bearing on the relation between the plant's morphological response to its environment and its chemical composition.

METHODS

Seed of the varieties Hard Federation (a spring wheat), Turkey (a hard red winter wheat), and Harvest Queen (a soft red winter wheat which is intermediate in its response to temperature) were sown on December 5, 1927, in each of three greenhouses at the Arlington Experiment Farm, Rosslyn, Va. These greenhouses were maintained at different temperatures, referred to as low, medium, and high, respectively. The benches on which the plants were grown were located in the same relative positions in each house so that light conditions were the same for all. The soil moisture was kept as uniform as possible throughout.

The temperatures were approximately controlled by hand regulation of the steam valves and ventilators. The air-temperature ranges were roughly 12°–18° C. in the low-temperature house, 20°–25° in the medium-temperature house, and 25°–30° in the high-temperature house. The corresponding soil temperatures were approximately

[1] Received for publication Mar. 19, 1929; issued September, 1929.
[2] Reference is made by number (italic) to "Literature cited," p. 349.

12°–15°, 18°–20°, and 23°–25°. At night the temperatures of both soil and air usually dropped to the lower limit of each range and sometimes below on cold nights. Until near the end of March the upper limits were exceeded only occasionally on warm afternoons. During April, however, only intermittent control of the low-temperature and medium-temperature houses was possible. The experiment was concluded early in April, therefore, when the plants were 18 weeks old.

The leaves of the plants selected for the determinations were ground to a pulp in a Nixtamal mill. The juice was expressed by squeezing it through cheesecloth. Its hydrogen-ion concentration and titratable acidity[3] were determined electrometrically according to methods described previously (*6*). The specific gravity of each sample of juice was determined by means of a small pycnometer. In order to clarify the portion of juice used for this measurement, it was heated to 60° C. before filtering. The percentage of dry matter in the leaves was determined by drying samples to practically constant weight at 100° C.

In order to obviate the effects of diurnal changes in the composition of the plants, they were always cut at about 10 o'clock in the morning. The measurements were made as quickly as possible in the sequence of cutting, in order to minimize changes in the juice on standing.

The plan of sampling throughout most of the experiment was to select plants of one variety growing at each of the three different temperatures for the samples taken on any one day. The corresponding measurements for the other two varieties were made on the two following days, or as soon thereafter as possible. The final values, obtained when the plants were 18 weeks old, were determined in a different order. To emphasize at this time the comparative effects of each temperature on the three different types of wheat, plants of the three varieties growing at one temperature were taken each day, until the plants at all three temperatures were sampled.

Similar sampling plans were followed for the corresponding dry-weight determinations, although these were not always made on leaves cut on the same day as were the leaves for the juice samples.

RESULTS

Hard Federation, the spring wheat, grew vigorously and yielded well at both the low and the medium temperatures (12°–18° and 20°–25° C.) and was the only variety to produce heads at the high temperature (25°–30°). The heads produced at the high temperature were mostly sterile, however, and the plants were very much stunted. (Fig. 1.) Turkey, the winter wheat, grew normally at the low temperature, but it grew so poorly at the medium temperature that it produced only a few heads, and at the high temperature it did not develop beyond the tillering stage. Harvest Queen grew normally at the low temperature, but heading was retarded and irregular at the medium temperature. Its development was so inhibited by the high temperature that it produced no heads, many of the plants never progressing

[3] The term "titratable acidity" is used to indicate the quantity of N/20 NaOH required to bring the reaction of 10 c. c. of juice to pH 8.3, the phenolphthalein end point.

beyond the tillering stage. Some reached an early shooting stage at the age of about 22 weeks, but none developed farther.

In Table 1 are given the hydrogen-ion, titratable-acid, and specific-gravity measurements and the dry-weight percentages for the leaves

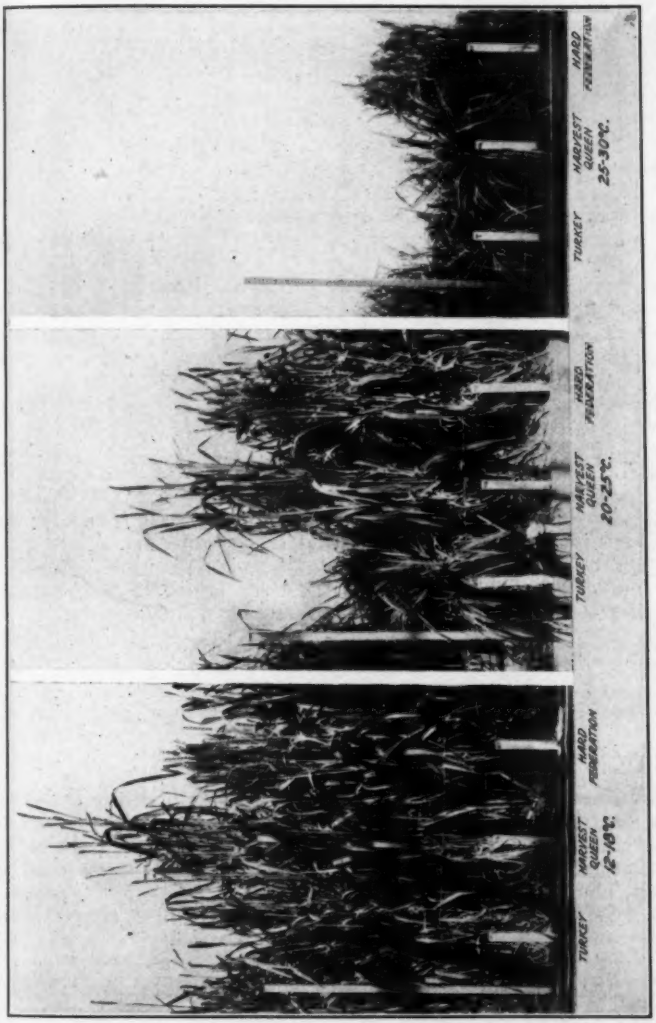

FIGURE 1.—Effects of three different temperature ranges on the growth of Hard Federation (a spring wheat), Turkey (a winter wheat), and Harvest Queen (a winter wheat which was somewhat intermediate in its temperature relations). Plants 22 weeks old

of representative plants of each lot, selected at intervals between the early tillering stage and the cessation of temperature control at the age of 18 weeks.

TABLE 1.—*Comparative effects of different temperatures on the acidity and specific gravity of leaf juice and on the percentages of dry matter in the leaves of plants of certain spring and winter wheat varieties*

[Roman type = tillering stage; italic = shooting stage; boldface = period of head formation]

Age (in weeks)	Spring wheat (Hard Federation)			Intermediate (Harvest Queen)			Winter wheat (Turkey)		
	12°-18° C.	20°-25° C.	25°-30° C.	12°-18° C.	20°-25° C.	25°-30° C.	12°-18° C.	20°-25° C.	25°-30° C.
	pH values								
5	6.25	6.02	6.04	6.15	6.04	5.94	6.16	6.04	5.91
8	6.08	*6.01*	5.90	6.11	5.98	5.92	6.19	6.09	5.84
9	*6.16*	*6.10*	*6.04*	6.07	*6.02*	5.84	6.12	5.90	5.86
12	*6.12*	*6.04*	*5.96*	*6.09*	*6.04*	5.80	6.01	5.95	5.79
15-16	**6.11**	**6.10**	**5.79**	*6.01*	*5.90*	5.64	*5.89*	5.85	5.63
18	**6.13**	**6.07**	**5.74**	**5.94**	*5.85*	5.65	*5.84*	*5.65*	5.62
	Titratable acidity (c. c. N/20 NaOH to neutralize 10 c. c. of juice)								
5	9.3	7.7	9.4	9.1	7.1	8.0	9.9	7.7	9.6
8	7.4	*7.1*	9.6	7.3	6.8	8.6	7.5	6.4	9.5
9	*7.0*	*5.9*	*7.6*	7.7	*6.1*	8.6	8.4	7.6	8.7
12	*5.7*	*6.1*	*8.4*	*7.2*	*5.6*	8.8	8.7	6.9	8.9
15-16	**8.5**	**7.5**	**10.6**	*8.1*	*7.6*	12.2	*9.2*	6.9	10.8
18	**8.4**	**8.4**	**13.3**	**10.0**	*9.0*	12.3	*11.1*	*9.7*	11.4
	Specific gravity of juice								
5	1.0328	1.0290	1.0374	1.0313	1.0269	1.0320	1.0289	1.0263	1.0288
8	1.0295	*1.0289*	1.0334	1.0271	1.0267	1.0307	1.0305	1.0266	1.0326
9	*1.0285*	*1.0213*	*1.0254*	1.0233	*1.0226*	1.0271	1.0271	1.0251	1.0271
12	*1.0253*	*1.0244*	*1.0302*	*1.0248*	*1.0223*	1.0296	1.0331	1.0259	1.0311
15-16	**1.0309**	**1.0289**	**1.0364**	*1.0278*	*1.0272*	1.0293	*1.0304*	1.0269	1.0317
18	**1.0278**	**1.0305**	**1.0391**	**1.0288**	*1.0283*	1.0335	*1.0292*	*1.0316*	1.0335
	Percentage of dry matter in leaves								
3[a]	12.53	10.84	13.69	12.45	10.19	12.93	13.88	11.28	13.59
5	15.10	13.96	16.62	14.54	12.21	15.09	13.84	12.40	14.46
8	13.65	*12.57*	15.59	12.67	12.08	15.79	14.02	12.81	14.42
9	*12.43*	*12.27*	*14.19*	11.65	*10.85*	13.13	14.21	12.94	13.80
12	*12.75*	*12.40*	*15.61*	*12.33*	*12.11*	13.91	15.60	12.16	14.62
15-16	**18.23**	**18.67**	**20.03**	*17.50*	*16.26*	18.71	[b]15.97	*14.81*	14.74	14.62
18	**18.08**	**18.30**	**24.47**	**16.64**	*16.37*	[b]15.97	*17.32*	*14.82*	15.05

[a] The dry-weight percentages at the age of 3 weeks were determined in connection with another experiment, but are included here because they were made on the same plants and under conditions comparable with those of the other measurements. No measurements on the juice were made at this time.

[b] Single determination; duplicate sample lost in drying.

DISCUSSION OF RESULTS

HYDROGEN-ION DETERMINATIONS

The pH values in Table 1 show the extent to which the hydrogen-ion concentration of the leaf juice of wheat is determined by the temperature at which the plants are grown. In each variety the lowest pH values were obtained for plants grown in the high-temperature house. The only exception was Hard Federation at the age of 5 weeks. Without exception, the highest pH values characterized plants grown in the low-temperature house.[4]

[4] In a later experiment (1929) a lower temperature range (approximately 11° to 14° C.) was maintained in the low-temperature house by means of automatic control devices. The rate of development of seedlings growing at this temperature was distinctly slower than that of the low-temperature seedlings of the experiment reported in this paper. Their pH values were lower (between 5.8 and 5.9) than those of the more rapidly developing seedlings of the next higher temperature (approximately 21° to 24° C.), which had values near pH 6.0. The experiment was repeated with similar results. So it seems that, although the hydrogen-ion concentrations of the present experiment all varied directly with temperature—a relation resulting from the fact that the best development occurred throughout at the lowest temperature—a still lower temperature range, one so low as to cause severe retardation of the seedlings, increases their acidity above that of seedlings grown at a more favorable temperature. This finding constitutes further evidence of the close relation between the pH value and the vigor of growth.

It has been found (*8*) that the hydrogen-ion concentration of the juice of healthy wheat plants growing under greenhouse conditions remains relatively low throughout the vegetative period and increases during the maturation period, reaching a relatively high value by the soft-dough stage. In the present experiment only those plants which were highly vigorous (low-temperature Hard Federation and Harvest Queen and medium-temperature Hard Federation) maintained their original low hydrogen-ion concentration (near pH 6.0) throughout their vegetative period. The hydrogen-ion concentration of those plants which were somewhat less sturdy (medium-temperature Harvest Queen and low-temperature Turkey [5]) increased after about three months; and that of plants which were markedly stunted and retarded (high-temperature Turkey and Harvest Queen and medium-temperature Turkey) began to increase at an earlier stage. Thus external manifestations of the unfavorable effects of the high temperatures were found to be associated with evidence of an unbalanced metabolism.

There was an evident relationship between the course of these changes in hydrogen-ion concentration and the degree of adaptability of the variety to the particular temperature. For instance, the winter wheats, Turkey and Harvest Queen, showed the first and most severe injury at the high temperature. Their hydrogen-ion concentrations rose sooner, and eventually to higher values, than did those of the spring wheat, Hard Federation, which was less injured by this temperature.

The medium temperature brought out most clearly the differences in the climatic adaptability of the three varieties. Here Hard Federation grew vigorously and maintained a normally low hydrogen-ion concentration throughout its development, whereas Turkey developed slowly and was characterized, as signs of injury became apparent, by increasing hydrogen-ion concentrations. Harvest Queen was intermediate with respect to its ability to develop at this temperature, and in its late stages, when retardation became apparent, it was intermediate with respect to hydrogen-ion concentration.

TABLE 2.—*The correlation between the hydrogen-ion concentration of the expressed juice of wheat and the vigor of the plants at the age of 18 weeks, as shown by their general appearance, stage of development, and height*

Condition of plants	Variety and habit	Temperature	Stage of development	Approximate height (cm.)	pH
Group 1: Highly vigorous; normal development.	Hard Federation (spring).	Low	Past flowering	130	6.13
	do	Medium	do	105	6.07
	Harvest Queen (intermediate).	Low	Heading	125	5.94
Group 2: Moderately vigorous; irregular heading.	do	Medium	Shooting	95	5.85
	Turkey (winter)	Low	do	85	5.84
Group 3: Injured; stunted growth; sterile heads.	Hard Federation (spring).	High	Past flowering	65	5.74
Group 4: Severely injured; development arrested at an early vegetative stage.	Turkey (winter)	Medium	Shooting	65	5.65
	Harvest Queen (intermediate).	High	Tillering	45	5.65
	Turkey (winter)	do	do	30	5.63

[5] The weaker growth of Turkey may have been partly due to shading, inasmuch as the adjacent rows of Hard Federation and Harvest Queen were taller throughout the experiment.

In Table 2 the pH values obtained at the age of 18 weeks, when the experiment was concluded, are grouped according to the relative degree of vigor of the plants at that time, as indicated by a comparison of their general appearance, stage of development, and height. In considering the data in this table in connection with the appearance of the plants shown by the photograph in Figure 1, taken four weeks later,[6] it should be noted that the lesser vigor of the plants in Group 2 as compared with those in Group 1 was obvious not only from their retarded development but also from their irregular heading which gave them a ragged appearance.

Table 2 shows the degree of correlation between the hydrogen-ion concentration and the relative vigor of each different lot of plants. The most vigorous plants all had pH values between 5.94 and 6.13, and the most injured ones all had pH values between 5.63 and 5.65. Reference to Table 1 will show that the plants in the most severely injured group had lower pH values than the rest at each sampling period after about the first two months. These high acid concentrations were evidently indications of the abnormality which resulted eventually in inability to produce heads.

It appears, then, that the absolute magnitudes of the pH values[7] reflected the physical condition of the plants. Values above pH 5.9 were obtained for healthy, vigorously growing plants regardless of variety. Values near 5.8 were obtained for moderately vigorous plants. Values as low as 5.65 were obtained only for slow-growing, extremely stunted plants.

There is considerable evidence that a slight increase in hydrogen-ion concentration often occurred before the adverse effects of an unfavorable environment could be ascertained by visual inspection. The plants with pH values as low as 5.9 in early stages of development were all considered healthy but they showed subsequently a diminution in vigor. Apparently, under the conditions of this experiment, a value near 5.9 during the vegetative period constituted a prediction of the subsequent appearance of symptoms of injury or retardation.

The conclusions of this experiment, in so far as they relate to absolute pH values, probably can not be extended to situations where the environmental complex is different. Light and soil conditions, as well as temperature, affect the hydrogen-ion concentration and determine the normal values for a given set of conditions (*1*, *4*, *5*, *10*, *11*, *15*). Thus the hydrogen-ion concentrations obtained for some of the best field plants at the Arlington Experimental Farm were considerably higher than those for the vigorous greenhouse plants. Field plants of Harvest Queen, Shepherd, and Purplestraw had pH values of 5.74, 5.72, and 5.75, respectively, during the shooting stage, when the most vigorous greenhouse plants all had pH values above 6.0. However, the field plants were shorter than these best greenhouse plants, and their leaves were narrower and their culms less thick. Perhaps the tall, broad-leaved greenhouse plants, with their low concentrations of hydrogen ions, should be considered abnormally

[6] The rapid elongation of the culms of Harvest Queen during these four weeks was responsible for the difference between the relative heights of the different lots of plants as given in Table 2 and as shown in Figure 1.

[7] It should be noted that these absolute values are only significant, from the standpoint of vigor, during the period of vegetative development and up to the time during the maturation period when the normal increase in hydrogen-ion concentration begins.

vigorous. At any rate, their pH values consistently reflected the apparent difference in their vegetative development as compared to that of the field plants.

The persistent association of high hydrogen-ion concentration with lack of vigor recalls the fact that abnormal acidity of animal fluids also is associated with injury. Van Slyke in his studies of acidosis (*16*) found that the normal reaction of blood is between pH 7.3 and 7.5, and that values below 7.0 or above 7.8 are incompatible with life. It is not unreasonable to suppose that the plant also is very sensitive to changes in the reaction of its tissue fluids. Of course it is impossible to conclude that the high hydrogen-ion concentrations found in unhealthy plants have a causal association with injury. They may be merely incidental.

TITRATABLE ACIDITY, SPECIFIC GRAVITY, AND DRY-WEIGHT PERCENTAGES

Unlike the hydrogen-ion concentrations, the titratable-acidity measurements were not directly correlated with the temperatures at which the plants were grown. (Table 1.) The lowest values were generally obtained for the medium-temperature plants, which had also the lowest specific-gravity measurements and dry-weight percentages, up to the time of the final measurements when poor temperature control made comparisons uncertain. Although wheat is a low-temperature plant (*2*, *14*, *17*), these plants grew more rapidly than those at either the lower or the higher temperature during early stages of growth. Dickson (*2*) and Tottingham (*14*) also found that in early stages wheat grows more rapidly at temperatures above the optimum for growth at later stages and for maturation.

Reed (*13*) states, in connection with his conclusion that rapid vegetative growth is associated with high water intake and low sap concentration, that soil moisture seemed to be the determining factor. In the present experiment, the relatively high water content of the medium-temperature plants could not have been due to a higher soil moisture. In fact, the soil often was drier and rarely appreciably wetter than the soil in the other houses.

Under the conditions of these experiments, the titratable acidity of the juice usually varied directly with the specific gravity; i. e., with the total concentration of solutes. This conclusion is borne out by the fairly high correlation coefficient, 0.7314, which is obtained on considering all the titratable-acid and specific-gravity data as a group, regardless of the temperatures at which the plants were grown. The degree of correlation of these measurements is shown graphically in Figure 2.

The high-temperature plants generally had the highest titratable-acid concentrations as well as the highest specific-gravity measurements and the highest percentages of dry matter. In general it may be said that plants grown at temperatures so high that they are prevented from heading are characterized by higher acidity measurements and lower water content than are plants that develop normally. However, the titratable-acid measurement did not vary so consistently with the external appearance of the plants as did the hydrogen-ion concentration, which, by virtue of the buffer system, is independent of dilution within fairly wide limits (*9*).

The inhibiting effect of high temperature on the growth and maturation of wheat, especially of winter wheat, is in agreement with the observations of Dickson (*2*), Tottingham (*14*), Pojarkova (*12*), and others. Dickson (*3*) found that a change in the type of metabolism occurs at about those temperatures at which the change in morphological response occurs. He found a progressive decrease in sugars and dextrins in wheat grown at temperatures above 16° or 20° C. Tottingham (*14*) points out that temperature determines the type of metabolism by controlling the equilibrium between certain anabolic and catabolic reactions. He suggests that, since the rate of respiratory activity doubles between the relatively low and high temperatures of 15° and 25°, respectively, while the increase in rate of assimilation is appreciably less, such an increase in temperature should decrease the carbohydrate-protein ratio. His analyses show low-temperature plants

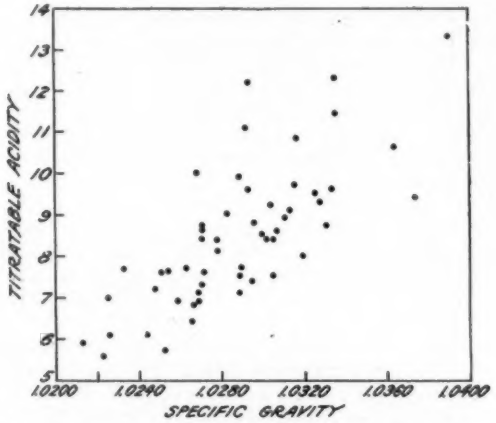

FIGURE 2.—Correlation between titratable acidity (c. c. N/20 NaOH) and specific gravity of wheat juice

to be characterized by a higher carbohydrate and protein content than are high-temperature plants.

It appears from the results of the present experiment that low-temperature plants are characterized also by lower hydrogen-ion concentrations than are high-temperature plants,[8] and that the extent of the increase in acidity induced by high temperatures is indicative of the susceptibility of the individual variety to injury at the given temperature. In other experiments it has been observed that not only high temperature but any condition that appreciably lowers the vigor of the plant (*6*, *7*, *8*) causes an increase in the acidity of the juice. At least in the case of wheat and corn it has been found to be generally true that a high degree of vegetative vigor results in normally low acid concentrations, and, conversely, that poor growth is associated with abnormally high concentrations.

[8] See footnote 4.

CONCLUSIONS

The concentration of hydrogen ions in leaf juice of Hard Federation, Harvest Queen, and Turkey wheats grown at temperatures of 12°–18°, 20°–25°, and 25°–30° C., respectively, was found to be lowest at the low temperature and highest at the high temperature.

The medium-temperature plants of all three varieties grew most rapidly at first, and almost without exception had the lowest titratable acidity, specific gravity, and dry-weight percentages throughout their vegetative stages, or as long as the temperature differences in the greenhouses could be maintained. The high-temperature plants generally had the highest titratable acidity, specific gravity, and dry-weight percentages.

The magnitudes of the titratable-acid values were closely correlated with those of the specific-gravity measurements at all three temperatures.

The pH value reflected the degree of adaptability of each variety to the different temperatures. Those plants which were best adapted, as shown by their vigorous growth and development, had pH values near 6.0 throughout the experiment. Those plants which were so injured that they failed to develop beyond the shooting stage developed much higher hydrogen-ion concentrations, extreme injury being accompanied by values near 5.6 while the plants were still in a vegetative stage.

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ADDITIONAL HOSTS OF FUSARIUM OXYSPORUM VAR. MEDICAGINIS [1]

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INTRODUCTION

In recent publications [2,3] the writer described a wilt disease of alfalfa caused by *Fusarium oxysporum* var. *medicaginis*, n. var. Since this fungus so closely resembles *F. oxysporum* morphologically and yet differs from it parasitically, it was thought that a further study of its host range should be made. With this in view, field and greenhouse experiments were conducted, the results of which are recorded in this paper.

GROWTH TESTS AT WEST POINT, MISS.

As the fungus is present in the soil of the Government experiment farm near West Point, Miss., it was thought desirable to grow different plants that might serve as hosts in this infested soil. H. L. Westover, agronomist in charge of the station, put at the writer's disposal one of the alfalfa plots in which the disease seemed to be most prevalent. Counts made of the plants from 3-yard-square sectors, one at each end and one at the center of this plot, showed that an average of 12½ per cent of the plants were infected. The crop of hay was removed and the ground was plowed and put into condition for planting. Two rod rows of each crop, located as far from each other as possible, were used in the test. Seeds of the following crops were planted on April 24, 1927. Acala cotton, Lone Star cotton, Early Black cowpea, Whippoorwill cowpea, Peking soy bean, Wilson Five soy bean, Tom Watson watermelon, Lespedeza, crimson clover, hairy vetch, white sweet clover, yellow sweet clover, black medic, white clover, Horsford's Market Garden pea, Oregon red clover, and tomato.[4]

Observations were made on these plots throughout the season by T. F. Akers, superintendent of the experiment farm, who sent plants suspected of having the disease to the writer. The experiment was discontinued on September 1, 1927, at which time all of the plants were pulled and the roots split open to determine if there was any evidence of vascular browning. Isolations were made from all plants showing discoloration in the bundles. Two of the tomato plants developed wilt, but *Fusarium lycopersici* was obtained from them.

[1] Received for publication Feb. 28, 1929; issued September, 1929. These investigations were conducted in cooperation with the Kansas Agricultural Experiment Station. Paper No. 288 of the Department of Botany and Plant Pathology, Kansas State Agricultural College.

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[3] WEIMER, J. L. A WILT DISEASE OF ALFALFA CAUSED BY FUSARIUM OXYSPORUM VAR. MEDICAGINIS, N. VAR. Jour. Agr. Research 37: 419-433, illus. 1928.

[4] Tomato plants purchased at the store; variety not known, but they were not resistant to *Fusarium lycopersici*.

Three of the red-clover plants showed typical vascular browning from which a species of Fusarium resembling *F. oxysporum* var. *medicaginis* was isolated. However, this fungus failed to infect alfalfa plants in subsequent trials. No Fusarium wilt was found in any of the other plants. Of the specimens sent by Akers, the alfalfa-wilt Fusarium was obtained only from hairy vetch. The infected plants were dying, and the stems showed some splitting and a little vascular browning. Isolations were made and a culture of what appeared to be *F. oxysporum* var. *medicaginis* was obtained. On one of his visits to West Point the writer found some garden peas and some common vetch plants which were dying and also showed evidence of vascular browning. Isolations were made from both the peas and the common vetch, and a fungus resembling *F. oxysporum* var. *medicaginis* in its cultural characters was obtained from each. These fungi, together with the one from hairy vetch, were later inoculated into alfalfa plants by inserting the spores and hyphae into wounds, and they produced 100, 100, and 90 per cent infection, respectively. The typical Fusarium-wilt symptoms were produced in the alfalfa plants, and the Fusarium was recovered in each case. This leaves little doubt that garden peas, common vetch, and hairy vetch, under certain conditions, may also serve as hosts for this species of Fusarium.

GROWTH TESTS AT MANHATTAN, KANS.

As a check on the experiments at West Point, Miss., similar tests were made at Manhattan, Kans. Here the soil was not infested with the fungus; hence the plants had to be inoculated. This was designed also as an alfalfa-variety test. Two rod rows of 16 different varieties of alfalfa as well as one row of each of the following plants were planted on a uniform piece of well-drained clay soil: Lespedeza, black medic, hairy vetch, white clover, yellow sweet clover, white sweet clover, Oregon red clover, crimson clover, *Vicia sativa*, Horsford's Market Garden pea, Midwest soy bean, Manchu soy bean, Trice cotton, Tom Watson watermelon, John Baer tomato, and Whippoorwill, Early Red, Early Buff, and Taylor cowpeas. In some cases one-half of one row and in other cases one-half of both rows of alfalfa were inoculated on June 7, 1927, by pouring a heavy spore suspension about the base of the plants. One-half of the plants of garden pea, soy bean, cotton, cowpea, and tomato were inoculated both by pouring a spore suspension about the plants and by inserting spores and hyphae into wounds in the tap root slightly below the surface of the soil. The remainder of the plants in each case were held uninoculated as controls.

The garden peas were pulled and examined on July 25. One plant which had been inoculated without wounding and three inoculated in wounds showed slight vascular browning. Isolations were made from three of the plants, and *Fusarium oxysporum* var. *medicaginis* was recovered from one of them, but not from the other two. This fungus produced wilt in alfalfa plants in a later experiment and was again recovered. There was no infection in any of the controls. These, together with the results obtained at West Point, show that the alfalfa-wilt fungus can cause a disease of garden peas. Only a comparatively small percentage of infection was obtained, and the vascular browning was rather slight in extent and seemed to be lim-

ited largely to the root. The plants infected remained small, and the leaves withered and died, those below dying first.

No infection was found in any of the other plants, except in one alfalfa plant of the Grimm variety. The fact that only one alfalfa plant became infected indicates that conditions were not very suitable for infection. However, not all of the perennial plants were pulled, the presence or absence of infection being judged by the top symptoms.

A further test of the susceptibility of different varieties of alfalfa was made by reinoculating the same lots of plants in June, 1928. The fungus used was grown on sterilized oats in 1-liter flasks, so that a large quantity of inoculum was available. Ten plants of each variety were inoculated by inserting spores and hyphae beneath the bark of the taproot near the crown. Other plants were inoculated by pouring the infested oats into a trench about the crowns of the plants and covering them with soil. The number of plants inoculated varied with the variety. In some cases only about 10 were available, whereas in others probably as many as 100 were used.

On September 7, 1928, all of the inoculated plants were dug, and the roots were cut open and examined carefully for the presence of vascular browning. All of the diseased plants were sectioned and studied microscopically, and abundant hyphae were found in the tracheal tubes. No isolations were made, as typical symptoms together with the presence of abundant hyphae in the ducts were considered sufficient evidence of the presence of the wilt disease. Only five plants in all were infected. Two of these were of the Grimm, two of the Hardigan, and one of the Turkestan variety.

Since only one plant was infected in 1927 and five in 1928, no conclusions can be drawn with respect to the comparative susceptibility of the varieties used. It seems apparent that some conditions at Manhattan, Kans., are not suitable for the infection of alfalfa by the wilt fungus.

SUMMARY

Hairy and common vetch and garden peas have been found to be susceptible to *Fusarium oxysporum* var. *medicaginis*, the alfalfa wilt-producing fungus.

An attempt was made to study the comparative susceptibility of 16 varieties of alfalfa under field conditions at Manhattan, Kans., but the plants that became infected were so few in number that no conclusions could be drawn.

VITAMIN CONTENT OF HONEY AND HONEYCOMB[1]

By HILDA BLACK KIFER, *Junior Nutrition Chemist*, and HAZEL E. MUNSELL, *Senior Nutrition Chemist, Bureau of Home Economics, United States Department of Agriculture*

INTRODUCTION

Honey has been considered a valuable food since earliest times. Consisting as it does of a mixture of dextrose and levulose it is easily digested, and this fact may account in part for the good results obtained when it is used in the diet, especially in infant feeding. Since honey can be used to advantage in the diet of infants the question arose as to whether it might not be a source of some or all of the vitamins. A review of the literature revealed the fact that very little work had been done in the way of determining quantitatively the vitamin content of honeys.

REVIEW OF LITERATURE

Dutcher (*3*)[2] determined the vitamin B content of honey obtained while basswood and white clover were in full bloom, using pigeons in his work. The tests were made by absorbing the vitamin of the honey on Lloyd's reagent and feeding amounts equivalent to 45 gm. of honey. Nectar was tested in the same manner. Dutcher concluded that the strained honey contained a negligible amount of vitamin B and that there was little evidence of its presence in nectar.

In 1919 Bachman (*1*) found that 25 c. c. of a strained honey added to 75 c. c. of water and used in Nagel's solution did not furnish the vitamin necessary for the growth of yeast.

Faber (*4*) in 1920 made a study of the antiscorbutic value of a white-sage comb honey which was extracted before using. Guinea pigs were used, and all of them exhibited characteristic scurvy symptoms when fed a solution of 1 part of honey to 15 parts of water, which was later increased to 1 part of honey to 5 parts of water. The quantity of honey consumed ranged from 0.88 to 5.58 c. c. of honey per 100 gm. of initial body weight. Faber concluded that it was "probable" that honey contained no antiscorbutic vitamin.

Hawk, Smith, and Bergeim (*5*) determined the vitamin A, B, and C content of blended honey, white-clover honey, and honeycomb. For vitamin B their method consisted in feeding three groups of rats, respectively, (1) a diet free from vitamin B; (2) one in which blended honey replaced part of the starch; and (3) one in which white-clover honey replaced part of the starch. At the end of four weeks the diets were changed. Group 1 was divided and half the rats were given blended honey and the other half white-clover honey. After another two weeks all were given milk. From the results obtained, Hawk and his associates concluded that there was a small amount of vitamin B present in these honeys. Following a similar procedure for the

[1] Received for publication Feb. 12, 1929; issued September, 1929. These studies were carried on with the cooperation of the Bureau of Entomology, U. S. Department of Agriculture.

[2] Reference is made by number (italic) to "Literature cited," p. 366.

vitamin A determination, they found that strained honey contained no vitamin A, whereas a definite but minimal amount was present in the comb honey. For the vitamin C test they fed three groups of guinea pigs in the same way; that is, they gave one group the scorbutic diet, a second group the same diet with blended honey to replace a part of the starch, and a third group the same diet with clover honey to replace the starch. All developed scurvy within two weeks, showing that the honeys contained no vitamin C.

In 1922 Luttinger (*6*) gave a general report of his findings on the use of honey in infant feeding in which he states that he found vitamins A, B, C present in 82 per cent of the honey examined. No experimental evidence was presented to bear out this statement.

Scheunert, Schieblich, and Schwanebeck (*8*), in 1923, examined three samples of honey for vitamins A, B, C, and concluded that none of the samples contained vitamins.

Caillas (*2*), in 1925, reported work done with pigeons which seemed to show that fresh honey contained vitamin B. The number of birds used, however, was too small to make the results very convincing.

DESCRIPTION OF HONEYS TESTED

Since it was out of the question to make an exhaustive examination of honeys of all the principal floral sources, three samples representing the extremes of color variation were chosen for investigation. None of the honeys had been heated as is often the case with extracted honey. Honey No. 1 was a white-clover honey from Grover Hill, Ohio. This was in a granular state when received. Honey No. 2 was a buckwheat honey, very dark in color, produced near Varysburg, N. Y. Honey No. 3 was a light-colored white-clover honey from Middlebury, Vt. It was drained from the comb and the comb was pressed as free from adhering honey as possible and was also used in feeding tests.

EXPERIMENTAL DATA

VITAMIN A DETERMINATIONS

The method used for vitamin A determinations was essentially that of Sherman and Munsell (*11*) with a few modifications.

The basal diet consisted of casein (purified), 18 per cent; starch, 67 per cent; brewery yeast, 10 per cent; Osborne and Mendel salts, 4 per cent; table salt, 1 per cent. The diet was irradiated with the light from a mercury vapor quartz lamp to insure an abundance of vitamin D. The rats were fed the vitamin-A-free diet until stationary or declining weight and appearance of symptoms due to vitamin A deficiency indicated that their body stores of vitamin A were depleted. As soon as the rats were in a suitable condition to be used for tests they were weighed and placed in individual cages. A weighed amount of the vitamin-A-free food was given to each rat and the honey was fed as a daily supplement to this diet.

Honeys No. 1 and No. 2 were fed in amounts of 1, 2, and 3 gm. per day. The plan of feeding daily portions of honey to the rats required a great deal of time. For this reason honey No. 3 and the honeycomb were incorporated in the basal diet in place of 30 per cent of the starch. In each litter one or more animals were designated as controls and received only the basal diet during the test period. The test period was continued for eight weeks, or until it was terminated by

the death of the rat. If the rat did not live out the eight weeks the last recorded weight is that of the dead rat. Autopsies were performed on all animals to determine whether the gross pathological lesions shown by animals confined to a vitamin-A-free diet were present. Table 1 gives the weights and survival periods of the rats used for these tests. Curves showing the changes in weight made by averaging results from the groups of test animals are presented in Figure 1.

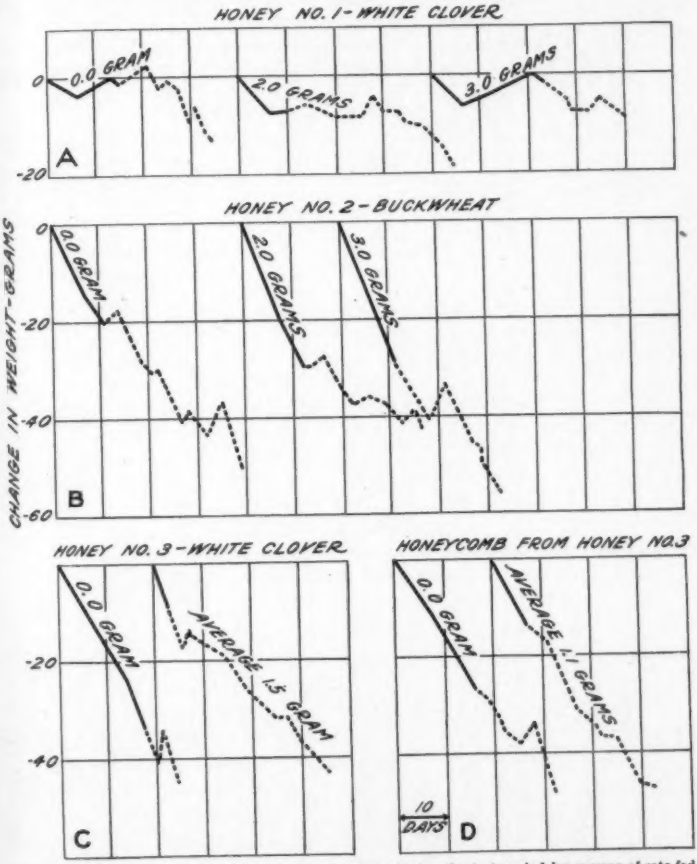

FIGURE 1.—Curves showing changes in weight made during the test period by groups of rats fed honey or honeycomb as the sole source of vitamin A. Each curve is the average result of several tests. The amount of honey or honeycomb received by each rat six times per week is indicated on each curve. The change in weight for the group is represented by a solid line to the point where the death of the first animal occurred. The broken line represents the averages for the surviving animals until all had died

None of the rats receiving the honey or honeycomb lived out the full eight weeks of the test period, nor did they live on an average any longer than the control rats. In all cases the rats fed honey and honeycomb exhibited as severe pathological lesions as those that received no honey in addition to the basal diet.

TABLE 1.—*Weight records of rats fed honey and honeycomb as the sole source of vitamin A*

WHITE-CLOVER HONEY (NO. 1)

Quantity of honey fed per rat per day, 6 days per week (grams)	Rat No.	Weight of rats at age of 4 weeks	Weight of rats when feeding of honey was begun	Weight of rats at end of successive weeks of test period								Period of survival
				1	2	3	4	5	6	7	8	
		Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
0	907	54	67	65	68	74	67	52				91
	922	50	65	62	63	71	54	50				84
	923	48	58	52	60	56	59	42				87
	937	51	66	64	68	78	77	54				84
	968	61	80	83	98	86	71					74
	975	54	71	68	88	85	77	60				83
	993	59	88	92	85	84	77	66				79
	996	52	77	70	74	70	66	50				79
	1110	36	80	69	56	53						57
	1123	45	85	78	75	76	58					59
Average												77.7
2.0	908	53	70	64	63	70	64	54				91
	921	46	55	53	51	57	53	45				91
	935	58	79	71	75	83	77	69				82
	972	56	61	53	49							59
	974	54	70	67	82	83	79	66	55	51		93
	994	57	83	77	77	60	61	57				79
	1107	64	116	95	95	75						63
	1120	45	92	84	80	79	60					61
Average												77.4
3.0	924	44	52	45	50	49	45					77
	925	42	50	45	48	52	44	36				84
	933	62	76	64	67	86	92	82	67			89
	934	52	66	58	60	67	62	49				84
	971	57	67	62	81	84	70	59				81
	995	55	86	84	77	76	60	58				78
	1119	46	95	88	83	78	77	71				67
Average												80.0

BUCKWHEAT HONEY (NO. 2)

0	1366	55	134	123	109	84						55
	1373	48	111	91	91	68	66					56
	1391	55	130	110	105	104	88	75				70
	1396	52	120	96	98	96	65					65
	1404	57	136	125	127	112	109	100	85			74
	1405	58	124	113	121	105	77					63
	1415	59	139	123	100							48
	1420	54	111	109	95	73						56
Average												60.9
2.0	1368	50	126	100	103	81	69					59
	1372	53	117	102	90	82	74	74				66
	1390	59	147	120	93	88						54
	1393	55	115	103	95	94	98	76	72			74
	1403	61	157	125	115	95	94					57
	1407	56	118	97	109	100	82	67				67
	1417	52	119	104	80							49
Average												60.9
3.0	1365	56	139	125	92	90						42
	1371	54	120	97	83	95	72	68				63
	1389	59	137	126	95	81						49
	1392	49	126	94	99	94	80	68				69
	1402	63	153	135	107	89						54
	1406	57	126	96	103	90	77					62
	1414	61	132	121	111	91						58
	1418	51	123	106	81							48
Average												55.6

TABLE 1.—*Weight records of rats fed honey and honeycomb as the sole source of vitamin A*—Continued

LIGHT-COLORED WHITE-CLOVER HONEY (NO. 3)

Quantity of honey fed per rat per day, 6 days per week (grams)	Rat No.	Weight of rats at age of 4 weeks	Weight of rats when feeding of honey was begun	Weight of rats at end of successive weeks of test period								Period of survival
				1	2	3	4	5	6	7	8	
		Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
0	3086	57	131	108	95	79						65
	3089	52	114	105	93	80	69					69
	3092	49	110	105	92	70						65
Average												66.0
Average, 1.5 (30 per cent of diet)	2903	63	137	101								54
	2904	62	120	113	109	89						67
	2906	57	134	94								54
	2907	58	98	87								51
	2909	55	118	109	96	94	76					76
	2910	54	115	85	95	85	84	72				83
	2911	50	106	82								54
	3085	57	125	118	98	94	80					70
	3087	50	104	87	84							53
	3088	56	123	105	108	90	92					72
	3090	51	105	95	90	78	76	64				76
	3091	50	117	100	87	80						66
	3093	40	100	94	91	83	63					72
Average												65.2

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0	3128	58	114	107	107	83	72					65
	3129	57	117	110	88	74						62
	3131	54	112	100	94	86	88	69				74
	3141	70	153	144	132	116	97					68
	3142	64	136	128	119	101	100	83				75
	3145	57	111	105	102	75	65					66
	3444	59	145	126	97	90						58
	3445	57	124	101	90	84						60
	3448	52	110	105	89	85	69					70
	3450	44	102	94	84	67	66					64
Average												66.2
Average, 1.1 (20 per cent of diet)	3125	61	134	112	100	86	84					64
	3127	59	122	110	107	86	72					70
	3130	56	114	105	92	78	74					67
	3132	47	106	96	82	63						59
	3144	60	130	119	96	95	84	76				73
	3143	54	111	107	94	74						62
	3146	57	117	110	92		85	70				76
	3446	55	120	80								49
	3447	52	114	95	86							53
	3449	52	103	100	85	79	65					67
Average												64.0

These results indicate that no one of these three samples of honey nor the honeycomb contained an amount of vitamin A that could be detected by the method used for measuring this factor.

VITAMIN B DETERMINATIONS

The determination of the vitamin B content of the three samples of honey was completed before the multiple nature of vitamin B had been generally recognized. The method used was that of Sherman and Spohn (*12*), which makes no distinction between the two vitamin B factors. All rats were kept in cages having raised screen bottoms and were given a basal diet of casein (purified) 18 per cent, starch 68 per cent, butterfat 8 per cent, cod liver oil 2 per cent, Osborne and Mendel salts 4 per cent. Honey No. 1 was fed in amounts of

1, 2, and 3 gm. per rat per day. The other two samples were incorporated in the basal diet and replaced 30 per cent of starch; the honeycomb replaced 20 per cent. The test period is usually eight weeks, but all of the animals used for these tests died before the end of the eighth week. The results are shown in Figure 2 and Table 2.

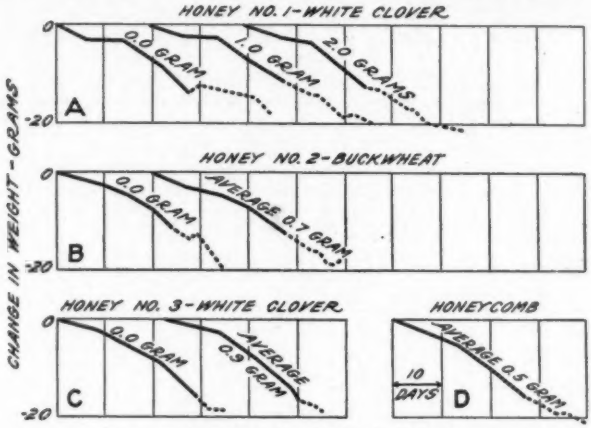

FIGURE 2.—Curves showing changes in weight made during the test period by groups of rats fed honey or honeycomb as the sole source of vitamin B. Each curve is the average result of several tests. The amount of honey or honeycomb fed to each rat six times per week is indicated on each curve. The change in weight for the group is represented by a solid line to the point where the death of the first animal occurred. The broken line represents the averages for the surviving animals until all had died

TABLE 2.—*Weight records of rats fed honey and honeycomb as the sole source of vitamin B*

WHITE-CLOVER HONEY (NO. 1)

Quantity of honey fed per rat per day, 6 days per week (grams)	Rat No.	Weight of rats at age of 4 weeks	Weight of rats at end of successive weeks of test period								Period of survival
			1	2	3	4	5	6	7	8	
		Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
0	988	46	38	37	34	25					28
	1142	44	40	40	37	37	34	29	26		45
	1304	50	51	49	44	39	33				35
	1398	50	50	52	45	35	33				30
Average											34.5
1.0	985	51	49	46	39	32					28
	987	48	46	45	37	30					28
	1137	47	41	44	41	38	33	30	27		46
	1143	37	32	35	31	28	25	24			36
	1305	45	49	41	37	30	28				34
	1307	48	46	50	47	37	34				35
	1397	51	52	51	45	40	36	31			42
	1400	50	45	47	42	37	33	28			40
Average											36.1
2.0	986	45	44	45	37	30					25
	989	44	41	39	33	27					28
	1138	47	41	40	37	34	30	26	25		46
	1139	42	37	35	33	29	25	23			36
	1303	50	51	48	40	39	32				35
	1306	50	54	48	41	35	30				34
	1399	49	44	46	40	36	32	30			36
	1401	50	47	47	40	35	31	28			37
Average											34.6

TABLE 2.—*Weight records of rats fed honey and honeycomb as the sole source of vitamin B*—Continued

BUCKWHEAT HONEY (NO. 2)

Quantity of honey fed per rat per day, 6 days per week (grams)	Rat No.	Weight of rats at age of 4 weeks	Weight of rats at end of successive weeks of test period								Period of survival
			1	2	3	4	5	6	7	8	
		Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
0	1961	45	41	41	36	30	26				34
	1968	41	40	36	31	25					26
	1972	41	39	37	33	27					28
	1985	35	34	31	27	25					24
	1989	32	32	29	26	21	19				30
Average											28.4
Average, 0.7 (30 per cent of diet)	1962	44	41	42	38	33	27	26			38
	1963	42	41	38	35	31	25				34
	1964	48	45	44	41	35	29	27			38
	1965	46	41	37	35	31	28	28			39
	1966	45	40	39	35	30	26				33
	1967	42	40	38	35	27	25				31
	1969	32	30	28	27	23	20				35
	1970	44	39	37	33	25	22				32
	1971	44	41	39	35	29	24	24			36
	1973	41	38	36	33	29	25	25			36
	1974	39	38	34	31	26	22				33
	1984	35	30	31	27	23	21				30
	1986	34	33	34	30	25	21				30
	1987	33	30	30	27	21					28
	1988	32	32	30	28	24	23				32
	1990	37	35	32	29	28	23				35
	1991	35	31	31	27	23	21				31
	1992	34	31	32	29	24	21				30
Average											33.4

LIGHT COLORED WHITE-CLOVER HONEY (NO. 3)

0	3010	49	49	45	41	34	30				31
	3014	45	46	43	38	32	27				31
	3015	45	45	42	36	31	29				30
	3072	52	50	48	40	36	32				32
	3075	52	48	44	43	38	33	28			38
	3079	45	41	38	38	30	29				29
	3081	45	41	37	36	30	26				31
Average											31.7
Average, 0.9 (30 per cent of diet)	3009	50	52	49	44	38	33				31
	3011	48	50	49	41	34	33				30
	3012	47	47	45	40	33	30				30
	3013	49	50	47	42	35	31				30
	3016	45	47	44	40	32	30				30
	3071	55	56	51	46	39	36				35
	3073	52	52	50	44	38	35				31
	3074	53	49	49	43	35	32				30
	3077	48	46	44	42	38	33				31
	3078	48	43	42	38	33	29				31
	3080	45	40	39	34	31	27				31
Average											30.9

HONEYCOMB

Average, 0.5 (20 per cent of diet)	3173	50	48	45	39	34	31	29			40
	3174	50	48	45	38	33	29				34
	3175	47	43	42	35	32	28				34
	3176	45	44	41	36	30	28				33
	3177	48	45	42	35	31	28				33
	3178	47	45	41	34	31					27
	3179	46	44	39	34	31					28
Average											32.7

TABLE 3.—*Weight records and autopsy findings of guinea pigs receiving honey as the sole source of vitamin C*

Guinea pig No.	Honey fed per 300 gm. of initial guinea pig weight	Weight of guinea pig			Duration of experiment	Type of scurvy symptoms at autopsy	Autopsy findings *								Total of autopsy findings
		Beginning	Maximum	Final			Bony system				Hemorrhages				
							Jaw	Teeth	Ribs	Joints	Ribs	Intestines	Joints	Muscle	
	Grams	*Grams*	*Grams*	*Grams*	*Days*										
NO HONEY															
B 5	0	300	306	191	26	Severe	+++	+++	+++	+++	+++	++	+++	++	22
B 20	0	304	339	164	26	Very severe	+++	+++	+++	+++	+++	+++	+++	+++	24
B 40	0	344	350	184	23	Severe	+++	+++	+++	–	+++	+++	+++	++	20
Average					25.0										22
WHITE-CLOVER HONEY (NO. 1)															
B 11	1.82	310	310	227	20	Mild	++	++	++	++	–	+	Trace.	Trace.	9
B 37	2.78	347	359	196	28	Moderate	+++	+++	+++	+	Trace.	+	+	...do...	12
B 13	2.86	378	397	244	27	Mild	+	+	+++	+	–	+++	++	+	12
B 39	2.90	350	360	249	31	Severe	++	+++	+++	++	++	+	++	+	17
B 38	3.19	340	352	194	26	...do...	+++	+++	+++	++	+	+++	+++	++	20
B 35	3.28	402	406	206	27	Moderate	+	+++	+++	+	–	+	++	++	14
B 26	3.39	353	365	192	24	...do...	++	++	+++	+	+	++	+++	++	16
B 7	3.40	314	380	214	37	...do...	+	++	+	++	Trace.	++	+++	++	13
B 18	3.52	299	308	195	24	Severe	+++	+++	+	+	+++	Trace.	Trace.	Trace.	11
B 14	3.67	321	373	233	28	...do...	+	+	+++	+++	++	...do...	+++	+++	16
B 16	3.70	296	311	164	26	...do...	+++	+++	+++	++	+	+++	+	+++	19
B 1	3.82	306	353	201	35	...do...	+	++	+++	+	Trace.	+++	+	+	12
Average					27.7										14.3

BUCKWHEAT HONEY (NO. 2)

70	.74	414	428	252	29	Moderate	++	+++	++	+	−	+	++	+	12
71	.99	420	420	224	25	Severe	+++	+++	++	−	++	+++	++	++	17
67	1.04	419	420	298	21	Moderate	+	+	+++	+	++	+++	++	+	14
68	1.09	419	429	229	35	Mild	+++	+++	Trace.	Trace.	−	+	+	+	9
69	1.16	427	466	238	35	Severe	+++	+++	+++	+	++	++	++	+	17
64	1.20	413	443	243	32	do	+++	+++	+++	+	++	+	++	+	16
63	1.63	413	413	249	21	do	++	++	+++	Trace.	+++	+++	++	+	16
Average					28.3										14.4

LIGHT-COLORED WHITE-CLOVER HONEY (NO. 3)

75	.81	442	464	263	36	Severe	++	+++	+++	++	+	+++	++	++	18
73	.84	443	472	245	33	do	++	+++	+++	++	++	+++	++	++	19
76	1.20	453	461	291	29	do	+	+	+++	+	+++	++	+++	+++	17
74	1.42	437	453	261	25	do	+	++	+++	+	++	++	++	++	15
Average					30.8										17.3

[a] Intensity of scurvy symptoms is indicated by plus signs each having an arbitrary value of 1; minus signs indicate absence of symptoms.

No one of the honey samples nor the honeycomb enabled the rats to live any longer or to make any greater gains in weight than the rats that received no additions to the basal diet. These results show that the honeys and honeycomb examined contained no vitamin B.

VITAMIN C DETERMINATIONS

The method used to determine the vitamin C content of honey was that described by Sherman, LaMer, and Campbell (*10*). No tests were made on the honeycomb. The basal diet described by Sherman (*9*) consisted of skim-milk powder heated at 110° C. for 4 hours, 30 per cent; a mixture of equal parts commercial rolled oats and wheat bran, 59 per cent; butterfat, 10 per cent; table salt, 1 per cent. The guinea pigs were somewhat heavier at the beginning of the test period than the standard animal described by Sherman. Some difficulty had been experienced in other work in getting the smaller guinea pigs to eat the basal diet satisfactorily. In these tests the preliminary period was continued until it was ascertained beyond a doubt that the guinea pigs would eat the basal diet.

The honey was fed apart from the basal diet, and the test period was continued in each case until the guinea pig died. Honey is not relished by guinea pigs, and the feeding required a great deal of time and patience. The intake of honey was calculated as grams per day per 300 gm. of initial body weight. Table 3 gives the results of the feeding tests. For purposes of comparison each plus (+) under autopsy findings has been given a value of 1 and these have been totaled for each animal.

On an average the guinea pigs that had the honey did not live appreciably longer than those that had none. Before death and at autopsy all showed symptoms of scurvy that were as severe as the symptoms shown by the control animals. It is evident from these results that the three samples of honey examined contained no appreciable amounts of vitamin C.

VITAMIN D DETERMINATION

The method for testing for vitamin D is identical with that described in a previous paper (*7*). Young rats approximately 60 grams in weight were placed on the Steenbock low phosphorus diet consisting of yellow corn, 76 per cent; wheat gluten, 20 per cent; calcium carbonate, 3 per cent; and sodium chloride, 1 per cent, for 21 days, at which time they showed evidences of a rachitic condition. The honey was then fed during a test period of not less than 6 nor more than 15 days. At the end of the test period a line test was made according to the method described by McCollum (*15*). While this method may not be entirely satisfactory for quantitatively measuring vitamin D it seemed to us to be preferable to any other method worked out to date.

The three honeys tested were incorporated in the basal diet to the amount of 30 per cent, 10 per cent, and 20 per cent, respectively, and the honeycomb as 10 per cent. In each litter of rats used for testing honey No. 1 there was one or more control rats which were given 0.5 per cent cod-liver oil during the test period instead of honey. This plan of having positive controls was not considered necessary in the tests with the other samples.

Summaries of the results of these tests are given in Table 4. As all of the line tests with the honeys and the honeycomb were negative, the results with individual rats are not given. X-ray photographs were also made of the rats used in these determinations. These pictures check the line tests made on the corresponding rats in that all showed severe rickets. From these results it would seem that none of the honeys examined nor the honeycomb contained any amount of vitamin D that would cause calcium deposition in rats which had been maintained for 21 days on the Steenbock low-phosphorus-yellow-corn diet.

TABLE 4.—*Summary of tests made to determine the vitamin D content of honey and honeycomb as compared with a cod-liver oil supplement*

Test food in the diet (per cent)	Duration of test period	Number of cases	Average intake of honey per 100 gm. of rat per day	Average value of line test
	Days		*Grams*	
WHITE-CLOVER HONEY (NO. 1)				
0	0	11		0
	11	5		0
	13	6		0
	15	1		0
30.0	11	13	2.36	0
	12	2	1.98	0
	13	13	2.39	0
	15	1	2.49	0
COD-LIVER OIL				
0.5	9	15	0.04	4
	11	2	.04	4
BUCKWHEAT HONEY (NO. 2)				
0	0	4		0
	13	2		0
	15	4		0
10.0	11	2	0.70	0
	13	3	.67	0
	15	3	.70	0
20.0	13	2	1.45	0
	15	2	1.42	0
LIGHT-COLORED WHITE-CLOVER HONEY (NO. 3)				
0	0	3		0
	15	3		0
20.0	13	12	1.49	0
	15	12	1.50	0
HONEYCOMB				
0	0	1		0
	13	1		0
10.0	9	3	0.80	0
	13	3	.79	0

CONCLUSION

The three samples of honey examined were produced in widely separated localities and represented extremes of color variation. No detectable amounts of vitamins A, B, C, or D were found in any of the honeys or in the honeycomb.

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CORRELATED INHERITANCE IN A WHEAT CROSS BETWEEN FEDERATION AND A HYBRID OF SEVIER × DICKLOW[1]

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INTRODUCTION

Several wheat characters, such as culm length, spike density, and awn classes, have been shown to exhibit rather complicated inheritance. This paper reports a study of the inheritance and of the correlated inheritance of these and some other plant characters in a cross between Federation and a hybrid of Dicklow × Sevier (III C–18).

LITERATURE

The literature which applies to inheritance of the wheat characters herein reported has recently been rather thoroughly reviewed by Clark (*3*),[2] by Hayes and Garber (*5*), and by Stewart (*7*). For this reason only references which bear directly on the particular problems under discussion are cited.

DESCRIPTION OF PARENTS

Federation has been rapidly growing in importance in Utah and Idaho as an irrigated wheat. This is largely due to its high-yielding ability and to its habit of not lodging under irrigation. Its straw is short and stiff, and its glumes are dark bronze in color. It is classed as an awnless wheat (*4*), yet short-tip awns or beaks are usually present.

Different characters were measured on the 37 parent rows which were grown along with the F_3 progenies. The mean values for these are given below:

Length of longest culm to base of spike	cm	75. 34
Spike density—length of one rachis internode	mm	5. 02
Length of awn	do	5. 05
Neck thickness	do	2. 40
Culms per plant	number	10. 13

III C–18 is one of the high-yielding hybrid strains selected by Stewart at the Utah experiment station from a Sevier × Dicklow cross. It inherits to some extent, at least, the weak straw of its Sevier parent. Its glumes are white, and it is fully awned.

Measurements of plant characters of III C–18 in the 37 parent rows gave the following mean values:

Length of longest culm to base of spike	cm	91. 96
Spike density—length of one rachis internode	mm	2. 62
Awn length	do	73. 07
Neck thickness	do	2. 34
Culms per plant	number	9. 46

[1] Received for publication Jan. 30, 1929; issued September, 1929. Contribution from the Department of Agronomy, Utah Agricultural Experiment Station. Publication authorized by director, Jan. 25, 1929.

[2] Reference is made by number (italic) to "Literature cited," p. 392.

"The author is indebted to Dr. H. K. Hayes, of the Minnesota Station, for helpful criticisms in studying the data and arranging the manuscript. Dr. Fred Griffee of the Maine Station has also made several valuable suggestions."

These measurements show the culm length of III C–18 to be about 17 cm. greater than that of Federation. The spike is nearly twice as dense; the awns have considerable length. In neck thickness and in number of culms per plant the parents are almost alike.

EXPERIMENTAL PROCEDURE

The cross between a pure line of Federation and the pure line III C–18 was made in 1924 at Logan, Utah. The F_1 plants were grown in 1925, and the F_2 families in 1926. One of the most vigorous of these families was chosen to continue the experiment. The F_2 family chosen contained 354 plants. The plants were divided according to awn appearance into four groups, designated as awn class 1, 2, 3, and 4, or merely as awns 1, 2, 3, and 4. The plants in the group of awn class 1 had practically no awns at all, though most of them bore short beaks. At the apex of the spike there was an occasional short awn. Considerable care was taken to have this group correspond in awn development to that of the Federation parent. Plants belonging to awn class 4 were fully awned to correspond to the awn development of the other parent III C–18. The plants in awn class 2 bore intermediate awns with the principal awn development in the apical part of the spike. It was the intention to make this group correspond in awn development with that of the F_1 plants. The plants in awn class 3 were likewise intermediate in their awn development. The apical awns, however, were considerably longer than those of awn class 2, and short awns were found quite generally all the way down the spike. In awn class 2, on the other hand, the awns were limited largely to the apical third of the spike, with a few awn points below, but even these were almost entirely in the upper half of the spike.

Plants were separated into two classes for glume color, bronze and white. Spike density was obtained by measuring 10 internodes on a leading spike of each plant. The measurement was taken in the middle of the spike so as to avoid the internodes of irregular length both at the base and at the apex. The length of the longest culm was measured to the base of the spike. Awn length was obtained by measuring the length of one of the longest awns near the apex of each spike. The neck thickness was obtained by measuring with calipers the diameter of the culm in the thinnest place just below the spike. Care was taken not to crush the straw.

The data were so taken and recorded that all those from a given plant could easily be traced to that plant. This permitted the study of correlation.

Grains from each F_2 plant seeded an F_3 progeny row in 1927. Forty to fifty kernels spaced 3 inches apart were sown in each F_3 row except when an F_2 plant furnished fewer kernels than this. The rows were spaced 1 foot apart.

Since each F_2 plant seeded one F_3 progeny row, it was possible to use the breeding behavior of the F_3 progenies as the basis for classifying the F_2 plants. This method is definitely superior to the method of classifying the F_2 material, especially when studying complicated characters and characters which exhibit intermediate inheritance.

After each tenth progeny row the two parental varieties, Federation and III C–18, were sown side by side. These parental rows

were spaced and seeded in the same manner and at the same time as were the progeny rows. In all, there were 37 parental pairs. This procedure made it possible to study progeny characters in connection with parental characters.

When the grain was ripe each F_3 row was carefully harvested by pulling individually the plants in the row. The plants of each row were bundled, tied, and tagged. During the winter months each plant from each F_3 progeny and from each parental row was studied in the laboratory in the manner previously described.

The usual number of plants in each progeny ranged from 25 to 40. In some progenies there were fewer than this and in many there were 40 or more. In each row of the 37 pairs of parental rows there was a similar number of plants. Measurements and classifications were made on the basis of what the genetic material contained. No theory of inheritance was considered until all data were taken and tabulated.

EXPERIMENTAL RESULTS AND THEIR INTERPRETATION

After all the data were secured and recorded, studies were made of those concerned with each individual character and then with correlations between characters. Data regarding color of glume and also regarding awn classes could be readily grouped into homozygous and heterozygous progenies for study of inheritance of individual characters. The characters awn length, length of the longest culm, number of culms, spike density, and neck thickness involved a definite figure for each plant in an F_3 progeny. A mean value for each character measured was calculated, together with standard deviations and coefficients of variability. Studies of the comparative size of these constants showed whether it was possible to segregate the progenies into homozygous and heterozygous groups, or whether segregation could not be established. When the correlation studies were made the mean values of the F_3 progenies were the figures used, the mean of an F_3 progeny being regarded as more accurate than an individual figure from a single F_2 plant.

INHERITANCE OF INDIVIDUAL CHARACTERS

Inheritance studies were made of the following individual characters: Glume color, awn classes, awn length, length of longest culm, number of culms, and spike density.

Glume Color

Eighty-two F_3 progenies were homozygous for bronze glumes, 176 were heterozygous for color of glumes, and 96 were homozygous for white glumes. These numbers suggest the 1 : 2 : 1 ratio which has been previously observed by several other workers. There is probably a single-factor difference for color of glumes. The goodness of fit on this hypothesis is shown in Table 1. $\chi^2 = 1.1186$ and $P = 0.5782$, which is a good fit.

TABLE 1.—*Goodness of fit of three groups of F_3 progenies for glume color, compared with a 1 : 2 : 1 ratio*

[Grown in 1927 at Logan, Utah]

Progeny group	Calculated value (C)	Observed value (O)	O−C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Homozygous bronze	88.5	82	−6.5	42.25	0.4774
Heterozygous	177.0	176	−1.0	1.00	.0056
Homozygous white	88.5	96	+7.5	56.25	.6356

$\chi^2=1.1186$. $P=0.5782$.

AWN CLASSES

Figure 1 shows typical heads for each of four homozygous awn classes. Figures 2 to 5 show homozygous F_3 progenies for awn classes 1, 2, 3, and 4. Besides these homozygous classes there were five segregating classes of progenies, namely, those segregating for awn classes 1 and 2; those for awn classes 1, 2, and 3; those for awn classes 1, 2, 3, and 4; those for awn classes 2, 3, and 4; and those for awn classes 3 and 4.

FIGURE 1.—Type of awns found in the four awn classes of Federation × III C–18 wheat that are true breeding in the F_3 generation. In every case there is a somewhat greater awn development on the longer lax spikes. These classes are not purely theoretical; they were decided upon after a careful study of the F_3 progenies

There were, therefore, nine genotype classes into which the F_3 progenies were arranged in the following numbers:

	Progenies
1. Homozygous awn 4	23
2. Segregating awn 3, 4	38
3. Segregating awn 2, 3, 4	43
4. Segregating awn 1, 2, 3, 4	81
5. Homozygous awn 3	24
6. Segregating awn 1, 2, 3	46
7. Homozygous awn	24
8. Segregating awn 1, 2	50
9. Homozygous awn 1	25

These numbers suggest a ratio of 1:2:2:4:1:2:1:2:1, which would theoretically be obtained when 2-factor differences segregate independently.

Stewart (*7*) has suggested two linked factors with 35 per cent crossing over to explain the awn-class inheritance in Sevier × Federation

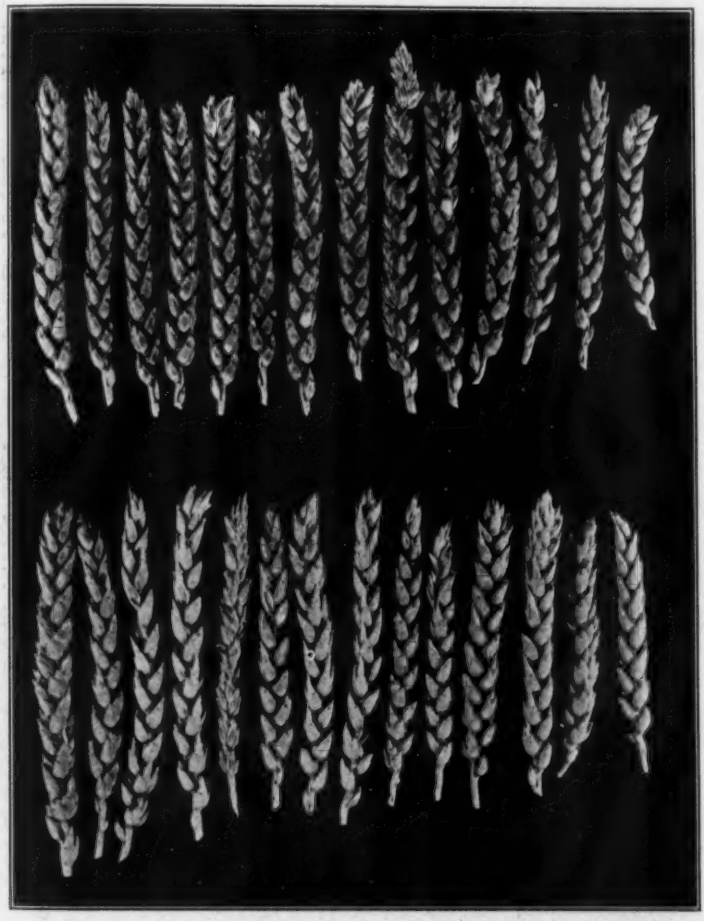

FIGURE 2.—One head from each plant of an F_3 progeny of Federation × III C–18 wheat breeding true for awn class 1. These plants are not really awnless but have a few short awn points. The Federation parent showed a similar range in awn points

crosses and in a cross between a Sevier × Dicklow hybrid (G 149) and Federation (*8*).

The awn-class inheritance in the Federation × III C–18 can be explained on a 2-factor difference only where independent segregation rather than linkage occurs, such as the Howards found in a cross

some years ago (*6*). This suggests that the hybrids III C–18 and G 149 both derived from Federation × Sevier crosses and both fully awned have different genetic constitutions for awn classes. One

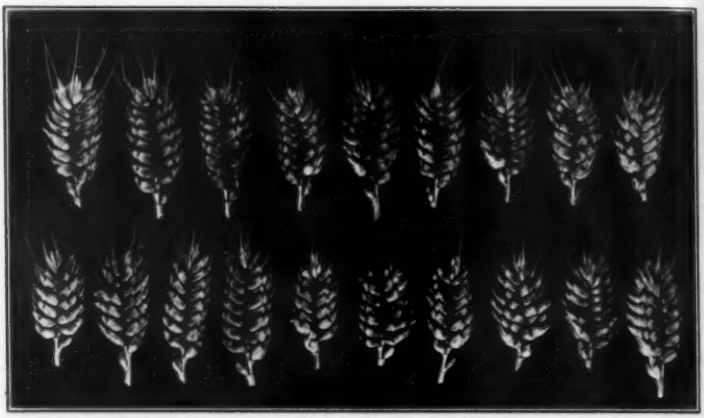

FIGURE 3. Representative heads from about half the plants of an F_2 progeny of Federation × III C-18 wheat breeding true for awn class 2; the entire range is shown. These spikes bear short awns, but they are limited to the upper spikelets

FIGURE 4.—Representative heads from plants of an F_2 progeny of Federation × III C-18 wheat breeding true for awn class 3. While some of these awns are quite long, none of them attain full length. The upper spikelets bear rather long awns while the middle and lower spikelets bear well-developed short awns and awn points

explanation which might be offered for this difference is that the Sevier variety of wheat is a composite of rather variable lines. One Sevier pure line when crossed with Dicklow may have given the strain which behaves like G 149, while another Sevier pure line crossed

with Dicklow may have given the III C–18 strain which behaves differently.

Since Federation × III C–18 shows no linkage, the assumption is here made that at least one of the awn factors in III C–18 is different

FIGURE 5.—Representative heads from plants of an F_3 progeny of Federation × III C–18 wheat breeding true for full-length awns of class 4. Long awns are borne on all spikelets except those at the very base of the spike. The lax spikes have the longer awns

from that in G 149. The factors designated for the Federation × G 149 cross (*4*) were *A* (*a*) and *T* (*t*). This use of the dominant factors to indicate the presence of awns does not follow Biffen (*1*) and others, who have regarded lack of awns as the dominant condition.

When the F_1 condition is as nearly intermediate as in the case of awns in wheat, there seems no real reason for not using the dominant to represent the presence of the positive character. For the Federation × III C–18 cross, let it be supposed that the factor *A* is the same as in the above cross but that *T* is not operative and is designated as *tt*, but that the factor *B* acts the same as *T* except that it is not linked with *A*. The awn classes would then be designated as follows:

Awn 4 = *AA tt BB*
Awn 3 = *AA tt bb*
Awn 2 = *aa tt BB*
Awn 1 = *aa tt bb*

TABLE 2.—*F_2 awn-class genotypes, their expected proportions on an independent segregation basis, and their expected breeding behavior*

No.	Genotype	Expected proportions	Expected breeding behavior
1	AA tt BB	1	Breed true for awn class 4.
2	AA tt Bb	2	Segregate for awn classes 3, 4.
3	Aa tt BB	2	Segregate for awn classes 2, 3, 4.
4	Aa tt Bb	4	Segregate for awn classes 1, 2, 3, 4.
5	AA tt bb	1	Breed true for awn class 3.
6	Aa tt bb	2	Segregate for awn classes 1, 2, 3.
7	aa tt BB	1	Breed true for awn class 2.
8	aa tt Bb	2	Segregate for awn classes 1, 2.
9	aa tt bb	1	Breed true for awn class 1.

Table 2 shows the nine F_2 awn-class genotypes, their expected ratio, and their breeding behavior based on the above assumption. The goodness of fit between the observed data and the expected frequencies is given in Table 3. On the basis of nine segregating classes, $\chi^2 = 3.0961$ and $P = 0.9270$, which is an extremely good fit. A worse fit due to chance alone is to be expected in 93 out of 100 cases.

TABLE 3.—*Goodness of fit of nine awn-genotype classes of F_3 progenies when compared with a 1 : 2 : 2 : 4 : 1 : 2 : 1 : 2 : 1 ratio which would theoretically be obtained when a 2-factor difference segregates independently*

[Grown in 1927 at Logan, Utah]

Calculated value (C)	Observed value (O)	O−C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
22.125	23	+0.875	0.7656	0.0346
44.250	38	−6.250	39.0625	.8828
44.250	43	−1.250	1.5625	.0353
88.500	81	−7.500	56.2500	.6356
22.125	24	+1.875	3.5156	.1589
44.250	46	+1.750	3.0625	.0692
22.125	24	+1.875	3.5156	.1589
44.250	50	+5.750	33.0625	.7472
22.125	25	+2.875	8.2656	.3736

$\chi^2 = 3.0961$. $P = 0.9270$.

It is interesting to note the resulting numbers in the four awn classes when the F_2 population was classified. The 354 F_2 plants were classified in 1926–27 before planting time just as were the F_3 progenies a year later. The numbers obtained for each of the awn-class groups were as follows:

Awn 4 = 49 F_2 plants
Awn 3 = 35 F_2 plants
Awn 2 = 106 F_2 plants
Awn 1 = 164 F_2 plants

These data when compared with the F_3 data indicate that the F_2 plants which will breed true in F_3 may resemble rather closely other F_2 plants which will segregate in the F_3 generation. In handling data of this sort it is much more accurate to classify the F_2 genotypes on the basis of their F_3 breeding behavior than on the basis of the appearance of the F_2 plants.

Awn Length

When the data on the F_3 progenies were first being secured it was thought to be unnecessary to measure the short-tip awns found on awn class 1 plants, but after about 90 of the progenies had been worked it was decided that this figure would be useful. The No. 1 awns were measured for the remainder of the progenies. Only the progenies in which all awn classes present were measured were used in making calculations of awn-length data. Since there was a fair representation in each awn-class group after eliminating the progenies in which the No. 1 awns were not measured, it is believed that the tables and calculations represent the material fairly accurately.

The mean awn length of the various awn classes together with their standard deviations and coefficients of variability are shown in Table 4.

Table 4.—*Mean length of the awns on progenies belonging to true-breeding awn classes 1, 2, 3, and 4 and to five segregating groups, together with the standard deviation (S. D.) and coefficient of variability (C.V.) for each awn-class group*

[Grown in 1927 at Logan, Utah]

Type of progeny	Mean awn length	Standard deviation	Coefficient of variability
True breeding for class:	*Mm.*	*Mm.*	*Per cent*
1	3.47	2.17	62.54
2	15.51	4.43	28.56
3	31.30	7.70	24.60
4	66.48	8.40	12.64
Segregating for classes:			
1, 2	7.33	5.52	75.31
1, 2, 3	19.05	12.92	67.82
1, 2, 3, 4	25.83	19.74	76.42
2, 3, 4	37.20	19.56	52.58
3, 4	48.06	16.36	34.04

Table 5.—*Awn-length classes of the means of parental rows and of F_2 progenies arranged according to coefficients-of-variability (C. V.) classes of the individual rows of each parent and of the 9 awn-class-genotype groups of the F_3 progenies*

[Grown in 1927 at Logan, Utah]

Parent or progeny	Number of plants in awn-length classes (millimeters)																	Total	C. V. classes
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5		
Federation	2	4																6	40.00
	7	9																16	60.00
	1	1																2	80.00
Total or mean	10	14																24	58.13
III C-18														4	23	8	1	36	10.00
															1			1	20.00
Total or mean														4	24	8	1	37	11.56

TABLE 5.—*Awn-length classes of the means of parental rows and of F_2 progenies arranged according to coefficients-of-variability (C. V.) classes of the individual rows of each parent and of the 9 awn-class-genotype groups of the F_3 progenies*—Continued

Parent or progeny	Number of plants in awn-length classes (millimeters)																		Total	C. V. classes
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5			
Homozygous for awn class 1	1																		1	40.00
	6	1																	7	60.00
	1																		1	80.00
	1																		1	100.00
Total or mean	9	1																	10	62.54
Segregating for awn classes 1 and 2	1		1																2	40.00
		5																	5	60.00
		14	1																15	80.00
	2	3																	5	100.00
	1																		1	120.00
Total or mean	4	22	2																28	75.31
Homozygous for awn class 2			7	10															17	20.00
			2	4															6	40.00
Total or mean			9	14															23	28.56
Segregating for awn classes, 1, 2, and 3				1	1														2	40.00
																				60.00
			5	3	1														9	80.00
			7	4															11	100.00
																				120.00
			2																2	140.00
Total or mean			14	8	2														24	67.82
Segregating for awn classes 1, 2, 3, and 4						1													1	40.00
						1	2												3	60.00
				9	8	8	3	1											29	80.00
				6	4	2													12	100.00
				3															3	120.00
Total or mean				18	12	12	5	1											48	96.42
Homozygous for awn class 3					1	7	7	2	4										21	20.00
						3													3	40.00
Total or mean					1	10	7	2	4										24	24.60
Segregating for awn classes 2, 3 and 4								1		1									2	20.00
							4	3	4	1									12	40.00
						3	6	9	5	1	1								25	60.00
					1		1	1											3	------
Total or mean					1	3	11	14	9	3	1								42	52.58
Segregating for awn classes 3 and 4									4	1	4								9	20.00
							1	3	3	10	5	5	1						28	40.00
								1											1	60.00
Total or mean							1	4	7	11	9	5	1						38	34.04
Homozygous for awn class 4									1		1	4	5	4	1	5	2		22	10.00
																			1	20.00
Total or mean									1		1	4	5	4	1	5	2		23	12.64

Table 5 shows the arrangement in awn-length classes and coefficient-of-variability classes of the nine awn-class genotypes. Standard deviation and coefficient-of-variability constants were both used in studying awn length. In the homozygous awn 1 group and in the awnless parent groups standard deviation seemed better to represent the true condition of the material on account of the very small mean awn length which unduly accentuated the size of the coefficients of variability. Usually the coefficient of variability is

the constant to use, and the one which was used for the classes shown in Table 5. It merely meets a mechanical difficulty in the case of the group ordinarily spoken of as awnless.

As shown in Table 6, homozygous-awn classes, except awn class 1, show a small range in coefficients-of-variability classes and also in mean coefficients of variability.

TABLE 6.—*Range of the coefficients of variability (C. V.) and mean coefficient of variability of awn length in the parent rows in the four homozygous awn classes and in the segregating awn classes*

[Grown in 1927 at Logan, Utah]

Rows or progenies	Range in C. V.	Mean C. V.
	Per cent	*Per cent*
Parental rows:		
Federation	39.8 to 70.7	58.13
III C–18	6.7 to 20.7	11.56
True breeding for—		
Awn class 1	42.7 to 103.0	62.54
2	17.9 to 33.4	28.56
3	18.7 to 32.0	24.60
4	7.7 to 25.6	12.64
Segregating for—		
Awn classes 1, 2	43.2 to 116.2	75.31
1, 2, 3	39.9 to 133.9	67.82
1, 2, 3, 4	45.2 to 123.2	76.42
2, 3, 4	23.8 to 84.8	52.58
3, 4	26.6 to 53.2	34.04

The segregating awn classes all show a greater range and a higher mean coefficient of variability than do the homozygous classes, except the awn 1 group, which has been discussed. It might be expected that the longer-awned classes would show a greater range and higher mean standard deviation but a smaller mean coefficient of variability than do the shorter-awned classes. This is borne out by the figures.

The higher coefficients of variability (C. V.) in segregating classes tend to show that eye classification of awn classes was fairly accurate. The coefficients of variability are from two to three times as great in the segregating classes as in the corresponding true-breeding classes.

In awn length the range of homozygous awn 1 progenies practically covers the range of the Federation parent, and the awn 4 progenies that of the III C–18 parent. The awn 1 progeny range is from 2.35 ± 0.96 to 5.39 ± 2.46 mm. Federation ranges from 3.56 ± 1.38 to 6.62 ± 2.77 mm. The awn 4 progenies range from 42.52 ± 7.35 to 80.40 ± 4.89 mm. in awn length, while the III C–18 rows range from 67.20 ± 9.30 to 84.50 ± 3.84 mm.

The homozygous awn 2 progenies range from 11.28 ± 1.59 to 19.68 ± 3.94 mm. in awn length. The homozygous awn 3 range is from 22.12 ± 3.71 to 42.15 ± 6.65 mm.

LENGTH OF LONGEST CULM

There was considerable difference between the lengths of the longest culm of the two parent plants. When the means of the 37 parental rows were averaged, the following figures were obtained: Federation = 75.34 cm. and III C–18 = 91.96 cm. The III C–18 parent is 16.62 cm. greater in culm length than is the Federation

parent. With this considerable difference between the parents, it could be expected that there would be a segregation in the F_2 generation and that there would be a tendency for the F_3 progenies to inherit the culm length of their respective F_2 parents.

TABLE 7.—*Culm-length classes of the means of Federation and III C-18 parental rows and of the F_3 progenies*

[Grown in 1927 at Logan, Utah]

Parent or progeny	Number of plants in culm-length classes (centimeters)													Total
	56	60	64	68	72	76	80	84	88	92	96	100	104	108	
Federation	1	----	1	3	8	11	9	3	1	----	----	----	----	----	37
III C-18	----	----	----	----	1	1	1	2	6	13	8	4	----	1	37
F_3 progenies	----	1	3	10	24	35	67	68	43	46	22	27	7	1	354

Table 7 shows the range in mean culm length for the parental rows and for the F_3 progenies. The parental classes overlap to some extent, but the shortest Federation row is four classes below the shortest III C–18 row, and the longest III C–18 row is five classes above the longest Federation row. Out of the 354 F_3 progenies the longest III C–18 row is practically recovered in one progeny. The longest III C–18 = 109.0 ± 3.95 cm. and the longest F_3 progeny = 107.75 ± 4.18 cm. The shortest Federation row is also practically recovered in one F_3 progeny. The shortest Federation row is 57.62 ± 3.72 cm. in culm length and the shortest F_3 progeny is 59.20 ± 4.40. The range of the progenies, then, essentially covers the range of the parents, and the distribution resembles somewhat that of a normal curve. (Fig. 6.) This study indicated segregation of culm length but did not establish the nature of culm-length inheritance.

The culm length of the F_2 plants was correlated with the mean culm length of their respective F_3 progenies. A correlation coefficient of +0.4316 ± 0.0291 was obtained. The constant is 14.8 times its probable error. This significant correlation obtained between the F_2 plants and their F_3 progenies indicates that segregation had occurred and that culm-length inheritance is displayed in this cross. This study did not find a means of separating the segregating groups.

NUMBER OF CULMS

The two parents average essentially the same number of culms per plant (Federation = 10.13 ± 1.37 and III C–18 = 9.46 ± 1.45). Correlation coefficients were calculated between number of culms in F_2 and F_3 and between all other plant characters studied. In every case the probable error was almost as large as its constant. In this cross, then, there seems to be no measurable segregation or inheritance in stooling ability as indicated by number of culms.

SPIKE DENSITY

As previously stated, the F_3 breeding behavior was used as the basis for determining the spike-density inheritance. The mean length of 10 rachis internodes of each F_3 progeny and of each parent

row was calculated. The coefficients of variability (C. V.) were also calculated and used as the basis for separating homozygous progenies from heterozygous. Table 8 shows the mean spike-density classes and the coefficient-of-variability (C. V.) classes of the parent rows and of the three groups of F_3 progenies, homozygous dense, heterozygous, and homozygous lax. Figure 7 shows the curves plotted for these same groups. Figure 8 illustrates the range in spike densities.

TABLE 8.—*Mean spike-density and coefficient-of-variability (C. V.) classes of Federation and III C–18 wheat, and of the three groups of F_3 progenies of their cross—homozygous dense, heterozygous, and homozygous lax* [a]

[Grown in 1927 at Logan, Utah]

Parent or progeny	Spike-density classes												Total	C. V. classes
	18	22	26	30	34	38	42	46	50	54	58	62	66	
Federation										1				1	4.00
									12	5				17	8.00
								4	12	2				18	12.00
								1						1	16.00
Total or mean								5	24	8				37	9.81
III C–18			15	1										16	8.00
			18	1										19	12.00
			2											2	16.00
Total or mean			35	2										37	10.59
Homozygous dense	2													2	4.00
	22	11												33	8.00
	16	22												38	12.00
	2	4	1											7	16.00
		1												1	20.00
Total or mean	42	38	1											81	10.70
Heterozygous			1	2			1							4	28.00
				4	5	3	1							13	32.00
		1	5	10	8	6								30	36.00
		1	11	20	19	4	1							56	40.00
		1	8	16	9	4								38	44.00
			3	8	8	2								21	48.00
				3	1	1								5	52.00
			1											1	56.00
			1				1							2	60.00
Total or mean		3	30	63	50	20	4							170	40.91
Homozygous									1					1	4.00
							2	8	18	25	7	2		62	8.00
							2	5	18	8	5		1	39	12.00
										1				1	16.00
Total or mean							4	13	37	34	12	2	1	103	9.56

[a] The vertical columns represent spike-density classes of the means of the parental rows and of F_3 progenies grouped horizontally by major groups into homozygous dense, heterozygous, and homozygous lax. The horizontal lines within each major group represent coefficients-of-variability (C. V.) classes. The mean coefficient of variability for each group is shown at the bottom of each group at the extreme right. The figures at the bottom of each group, on the "Total" line, are sums of the rows or progenies in that spike-density group. The figures in the second vertical column from the right (Total) are the sums of rows or progenies in that group falling within the coefficient-of-variability class designated.

The coefficients of variability of the Federation parent rows range from 7.47 to 14.65 per cent, with a mean of 9.81 per cent. The coefficients of variability of the III C–18 parent rows range from 4.9 to 14.14 per cent, with a mean of 10.59 per cent.

For the homozygous-dense F_3 progenies the range in coefficients of variability was from 4.78 to 18.12 per cent, with a mean of 10.7 per cent.

The coefficient-of-variability range in the homozygous-lax group was from 5.67 per cent to 15.16 per cent, with a mean of 9.56. Every progeny is clearly homozygous, as shown by its low coefficient of variability.

For the heterozygous F_3 progenies the range in coefficients of variability was from 27.42 to 61.28 per cent, with a mean of 40.91 per cent. Though there was one doubtful progeny, the actual range may be considered to be from 27 to 61 per cent. All these progenies have coefficients of variability sufficiently high to mark them clearly as heterozygous, whereas all the homozygous dense progenies have coefficients of variability sufficiently low to permit their ready classification as homozygous.

One progeny of only 13 plants gave a coefficient of variability of 17.19 per cent. This coefficient of variability indicates immediately that the progeny is true breeding. An examination of the plants themselves led to doubt in this respect. The lengths in millimeters of the

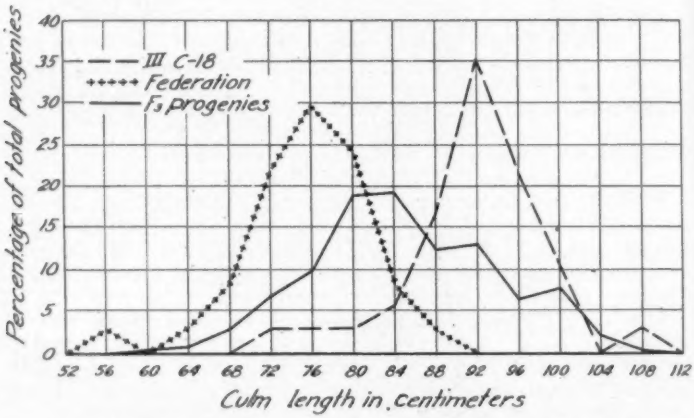

FIGURE 6.—Culm-length distribution curves of Federation and III C–18 parents and F_3 progenies; the entire culm-length range of both parents was recovered in the F_3 progenies

10 spikelet internodes on the 13 plants were 20, 24, 24, 27, 27, 29, 30, 30, 30, 33, 33, 35, and 40. None of the definitely true-breeding dense progenies show a range of 20 mm. in length of 10 spikelet internodes. The presence of just one very dense-spiked plant and just one long intermediate leaves the coefficient of variability small. This case illustrates the importance of having 30 or 40 plants in the progenies. When this progeny is regarded as being true breeding it is the only one in which the spike density of a progeny falls definitely within the range of the more compact parent, III C–18. In Figure 7 it is shown considerably toward the lax side from any other true-breeding dense progeny. The writers are far from sure that this progeny was not heterozygous. Since it was not continued in F_4, this was not definitely ascertained.

The means of the coefficients of variability of the two homozygous groups are nearly the same as the means of the parents. The range is also approximately the same. The heterozygous group has a much

higher mean and also a much wider range in coefficients of variability. Except for the one questionable progeny already discussed, the least variable heterozygous progeny is fully 50 per cent more variable than the most variable homozygous progeny, either of the dense or of the lax group. Such wide gaps establish the groups in clear-cut fashion.

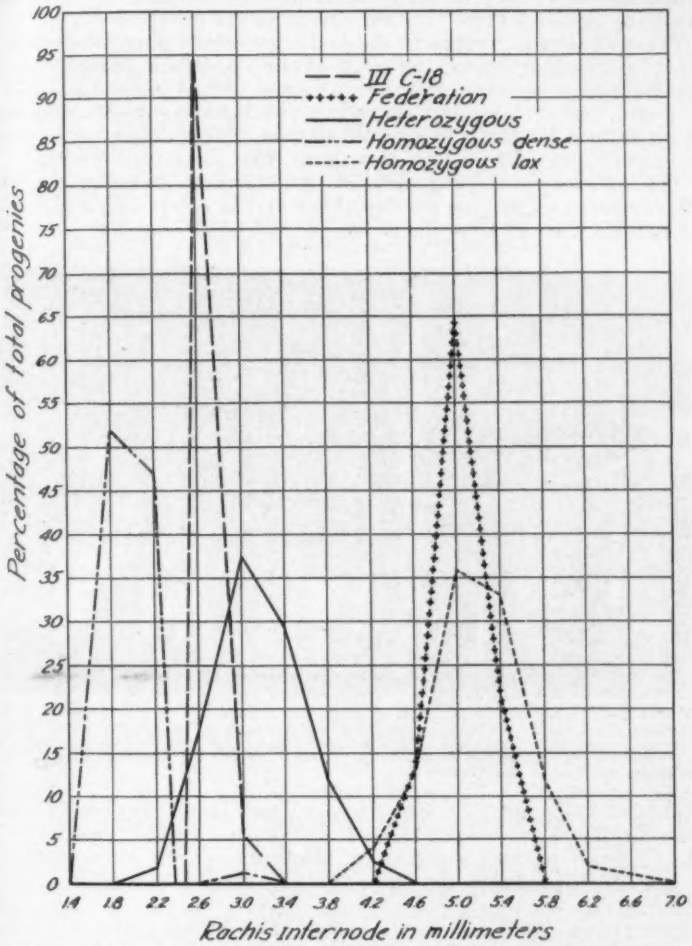

FIGURE 7.—Spike-density curves of Federation and III C-18 parents, and of three F_3 progeny groups—homozygous dense, heterozygous, and homozygous lax. Except for one progeny of doubtful breeding behavior the homozygous-dense progenies are all more dense than the more dense parent, III C-18

The range in spike density of the clearly homozygous-dense group of F_3 progenies is from 1.63 ± 0.10 to 2.37 ± 0.23 mm. per rachis internode. The most dense of the III C–18 parent rows was 2.41 ± 0.22 mm., which, it will be observed, is less dense (but not statistically

so) than the least dense of the homozygous-dense progenies. The mean density of the doubtful progeny was 29.38 ± 3.41 mm., which is definitely within the range of the more dense parent. The head density of III C–18 was not recovered except possibly in these two progenies, and perhaps not here. This is rather a peculiar situation which has occurred before in spike-density inheritance in crosses involving Sevier and Federation and is as yet unexplained.

The spike-density range in the homozygous-lax progenies seems to extend somewhat beyond the range of the Federation parent, though this is far from certain. Federation ranged from 4.66 ± 0.42 to 5.41 ± 0.18 mm. per rachis internode, while the homozygous-lax progenies range from 4.34 ± 0.33 to 6.40 ± 0.49 mm. The difference between 5.41 ± 0.18 and 6.40 ± 0.49 is less than twice the probable error.

The heterozygous progenies are intermediate between the two homozygous groups and overlap them in but a few cases, giving in the main a distinct trimodal curve.

FIGURE 8.—Spikes and rachis from parents and progeny of the Federation × III C–18 cross: A, Federation parent; B, III C–18 parent; C and D, spikes and rachis from the homozygous-lax F_3 progenies showing range of spike density; E and F, spikes and rachis from the homozygous-dense F_3 progenies showing range of spike density. C and D are from the most lax true-breeding F_3 progeny and E and F from the most dense

The F_1 spike density was 2.2 mm. per rachis internode. The heterozygous F_3 progenies came from F_2 plants which ranged from 1.6 to 2.8 mm. per rachis internode. Frequency curves of the F_2 parent plants which produced the three F_3 spike-density groups are shown in Figure 9.

There were 81 homozygous dense, 170 heterozygous, and 103 homozygous lax progenies. These numbers suggest a 1:2:1 ratio although $P = 0.1942$, which is only a fair fit. The goodness of fit is given in Table 9.

There is probably one major factor difference for spike density, and there may be some minor factors which modify this inheritance. This would seem to be indicated by the transgressive segregation which fails to recover the III C–18 parental head density (except in two cases at most, and not certainly in those) and by the rather wide range in the progenies of both homozygous groups.

TABLE 9.—*Goodness of fit of three groups of F_3 progenies for spike density compared with a 1:2:1 ratio*

[Grown in 1927 at Logan, Utah]

Progeny group	Calculated value (C)	Observed value (O)	O−C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Homozygous dense	88.5	81	−7.5	56.25	0.6356
Heterozygous	177.0	170	−7.0	49.00	.2768
Homozygous lax	88.5	103	+14.5	210.25	2.3757

$\chi^2=3.3288$, $P=0.1942$.

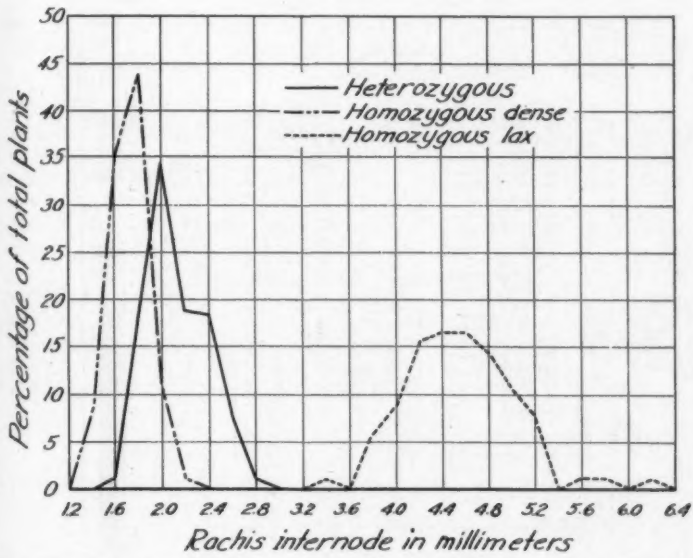

FIGURE 9.—Spike-density-distribution curves of F_2 plants which segregated in F_3 for the three major spike-density groups; the figure shows the spike-density curves of the F_3 progenies derived from these F_2 plants

CORRELATION OF CHARACTERS

AWN-CLASS AND SPIKE-DENSITY FACTORS PROBABLY NOT LINKED

Stewart (*9*) in a cross of Kanred × Sevier obtained high correlations between awn-length and spike-density characters. In a cross of Federation × Sevier (*8*) he obtained consistent correlation ratios (η) when spike density and awn classes were correlated. These results led to the belief that there was linkage between spike-density and awn-class factors.

In studying the present cross (Federation × III C–18) with respect to linkage for spike-density and awn-class factors, there are two points which should be borne in mind: (1) Awn class as separated by eye classification is a distinct and separate character from awn length. There might be a high correlation between awn length of

fully awned progenies and another plant character, while the correlation between awn classes and the same plant character could be low or even essentially zero. Different awn-class groups may have awn length correlated with a given plant character in quite different degrees, as will be seen later in this discussion. (2) The awn-class inheritance in the Federation × III C–18 cross is different from that of Federation × Sevier cross, as has been already shown. Inheritance in the former showed independent segregation on the basis of a 2-factor difference, while that of the latter showed linkage.

TABLE 10.—*Goodness of fit of 27 awn-class and spike-density genotype classes of F_3 progenies when compared with the theoretical ratio of independent segregation with 3-factor differences*[a]

[Grown in 1927 at Logan, Utah]

Class No.	Genotype	Calculated value (C)	Observed value (O)	O−C	(O−C)²	$\frac{(O-C)^2}{C}$
1	AA BB LL	5.53	6	+0.47	0.2209	0.0399
2	AA BB Ll	11.06	9	−2.06	4.2436	.3837
3	AA Bb LL	11.06	8	−3.06	9.3636	.8466
4	Aa BB LL	11.06	12	+.94	.8836	.0799
5	AA Bb Ll	22.12	26	+3.88	15.0544	.6806
6	Aa BB Ll	22.12	23	+.88	.7744	.0350
7	Aa Bb LL	22.12	24	+1.88	3.5344	.1598
8	Aa Bb Ll	44.24	38	−6.24	38.9376	.8801
9	AA BB ll	5.53	8	+2.47	6.1009	1.1032
10	AA Bb ll	11.06	4	−7.06	49.8436	4.5067
11	Aa BB ll	11.06	8	−3.06	9.3636	.8466
12	Aa Bb ll	22.12	19	−3.12	9.7344	.4401
13	AA bb LL	5.53	10	+4.47	19.9809	3.6132
14	AA bb Ll	11.06	8	−3.06	9.3636	.8466
15	Aa bb LL	11.06	15	+3.94	15.5236	1.4036
16	Aa bb Ll	22.12	19	−3.12	9.7344	.4401
17	aa BB LL	5.53	5	−.53	.2809	.0508
18	aa BB Ll	11.06	13	+1.94	3.7636	.3403
19	aa Bb LL	11.06	16	+4.94	24.4036	2.2065
20	aa Bb Ll	22.12	27	+4.88	23.8144	1.0766
21	AA bb ll	5.53	6	+.47	.2209	.0399
22	Aa bb ll	11.06	12	+.94	.8836	.0799
23	aa BB ll	5.53	6	+.47	.2209	.0399
24	aa Bb ll	11.06	7	−4.06	16.4836	1.4904
25	aa bb LL	5.53	7	+1.47	2.1609	.3908
26	aa bb Ll	11.06	8	−3.06	9.3636	.8466
27	aa bb ll	5.53	10	+4.47	19.9809	3.6132
	Total	353.92	354			

$\chi^2 = 26.4806$. $P = 0.4373$.

[a] *L*=lax spike and *l* dense spike; *A* and *B*=two factors for awns; *AABB*=fully awned condition.

In order to determine whether there was linkage between the awn-class and spike-density factors in the cross under study, the F_3 progenies were arranged into 27 genotype classes which would occur in independently segregating material where 3-factor differences are involved. Table 10 shows the genetic constitution of each of the 27 classes and also the goodness of fit when compared to the theoretical numbers which would be expected in a cross involving a 3-factor difference with independent segregation. The factor for lax spike is designated by *L* and its allelomorph dense spike by *l*. The awn classes have the same designation as before given.

For the 27 classes, $\chi^2 = 26.4806$ and $P = 0.4373$. This is a good fit, and indicates that there is at least no strong linkage between spike-density and awn-class characters in the Federation × III C–18 cross.

PARENTS

Correlations were calculated for the Federation and the adjacent III C–18 parental rows. The correlation coefficients, their probable errors, and the $r/P.E.$ are given in Table 11.

TABLE 11.—*Correlation coefficients* (r), *their respective probable errors* ($P.E.$), *and* $r/P.E.$ *for the pairs of parent rows when various plant characters were correlated*

[Grown in 1927, at Logan, Utah]

Plant character	r±P.E.	r/P.E.
Culm length	+0.5082±0.0318	16.0
Spike density	+.0865± .110	.8
Number of culms	−.4770± .0857	5.6
Awn length	+.0093± .1377	.1
Neck thickness	+.1240± .1092	1.1

The high positive correlation coefficient (r) obtained when the adjacent parental rows were correlated for culm length probably indicates that the soil heterogeneity influenced this character in a marked degree. The large minus correlation coefficient obtained when number of culms to the plant was considered probably indicates that a degree of competition existed between the two adjacent parental rows. Spike density ($r = +0.0865 \pm 0.110$), awn length ($r = +0.0093 \pm 0.1377$), and neck thickness ($r = +0.1240 \pm 0.1092$) seem to be more stable characters which are less influenced by environmental factors, as is shown by their low correlation coefficients.

Correlation coefficients were calculated for two pairs of plant characters studied for each parent. These constants with their probable errors are given in Table 12.

TABLE 12.—*Correlation coefficients* (r), *their respective probable errors* ($P.E.$), *and* $r/P.E.$ *for two pairs of plant characters on each parent*

[Grown in 1927 at Logan, Utah]

Parent and plant character	r−P.E.	r/P.E.
Federation:		
Culm length × spike density	−0.0118±0.1093	0.1
Spike density × neck thickness	+.6373± .0658	9.7
III C–18:		
Culm length × spike density	−.2436± .1043	2.3
Spike density × neck thickness	+.1877± .1070	1.8

Culm length × spike density in the Federation parent rows gave a correlation coefficient which is only one-tenth of its probable error ($r = -0.0118 \pm 0.1093$). These same two characters in the III C–18 give a correlation coefficient which is of little significance ($r = -0.2436 \pm 0.1043$).

In Federation, the correlation coefficient between spike density × neck thickness was large; that is, it was 9.7 times its probable error ($r = +0.6373 \pm 0.0658$). These same characters in the III C–18 gave a low correlation coefficient, which was only 1.8 times its probable error ($r = +0.1877 \pm 0.1070$). It seems from these data that spike density and neck thickness are distinctly correlated in the Federation parent. A laxer head tends to go with a thicker neck.

CORRELATION STUDIES WITH THE F_3 PROGENIES

Ten pairs of combinations of the five plant characters were possible. The correlation coefficients (r), the correlation ratios (η), and Blakeman's tests were calculated for all of the 10 pairs. These constants with their probable errors and $\frac{r}{P.E.}$ and $\frac{\eta}{P.E.}$ are given in Table 13.

TABLE 13.—*Correlation coefficients (r), correlation ratios (η), their respective probable errors (P. E.), and Blakeman's test for linearity for various pairs of plant characters for 354 F_3 progenies*

[Grown in 1927 at Logan, Utah]

Characters correlated	r±P. E.	r/P. E.	η±P. E.	η/P. E.	Blakeman's test
Culm length × spike density	+0.5198±0.0262	19.8	0.5344±0.0256	20.9	2.3740
Culm length × awn length	+.0584± .0417	1.4	.2993± .0381	7.9	3.5096
Culm length × neck thickness	+.1974± .0345	5.7	.2538± .0335	7.6	2.2263
Culm length × number of culms	+.0521± .0357	1.5	.1824± .0347	5.3	2.4427
Spike density × awn length	−.1112± .0413	2.7	.3496± .0367	9.5	3.9641
Spike density × neck thickness	+.4490± .0286	15.7	.5711± .0241	23.7	4.9302
Spike density × number of culms	+.0967± .0355	2.7	.1833± .0346	5.3	2.1760
Awn length × neck thickness	−.2874± .0384	7.5	.4068± .0349	11.7	3.4438
Awn length × number of culms	+.0343± .0418	.8	.3107± .0378	8.2	3.6926
Neck thickness × number of culms	+.0265± .0358	.7	.1755± .0347	5.1	2.4232

CULM LENGTH × SPIKE DENSITY

The correlation coefficient for culm length × spike density is large ($r = +0.5198 \pm 0.0262$). The constant is 19.8 times its probable error. The correlation ratio (η) is only slightly larger than r and Blakeman's test for linearity is only 2.3740, which indicates that the correlation is essentially linear in its nature.

Since this pair of characters when correlated in each of the two parents (Table 12) showed no significant constants, it was thought advisable to study the F_3 progenies more completely to determine, if possible, the nature of the relationship existing. In order to do this, the F_3 progenies were divided into their three spike-density groups—(1) homozygous dense, (2) heterozygous, and (3) homozygous lax. Correlations for culm length × spike density were then calculated for each of the three groups independently. The correlation coefficients (r), their probable errors (*P. E.*), and $\frac{r}{P.E.}$ are given in Table 14.

TABLE 14.—*Correlation coefficients (r) and probable errors (P. E.) for culm length × spike density in each of the three spike-density groups of the F_3 progenies*

[Grown in 1927 at Logan, Utah]

Spike-density group	r±P. E.	r/P. E.
Homozygous dense	+0.2454±0.0709	3.5
Heterozygous	+.1193± .0509	2.3
Homozygous lax	−.1612± .0648	2.5

Two of the groups, homozygous dense ($r = +0.2454 \pm 0.0709$) and heterozygous ($r = +0.1193 - 0.0509$) show comparatively small plus correlation coefficients, and the third group, homozygous lax, shows a small minus correlation coefficient ($r = -0.1612 \pm 0.0648$). The largest constant of the three is only 3.5 times its probable error. These constants indicate that the large correlation coefficient ($r = +0.5198 \pm 0.0262$) obtained when the entire 354 F_3 progenies were included is probably between groups (homozygous dense, heterozygous, and homozygous lax) rather than within the groups.

The spike-density factors seem strongly to influence culm length. This is somewhat in keeping with Boshnakian's findings (*2*). This is difficult to explain since the parental forms bring the characters into the cross in the opposite combination from that shown in the progenies. The lax-spiked parent (Federation) is the short parent and the dense-spiked parent (III C–18) is the tall parent. It has already been noted that spike-density inheritance is rather complicated. It may be that culm-length inheritance is also complicated.

Culm Length × Awn Length

The correlation coefficient between culm length and awn length is small ($+0.0584 \pm 0.0417$), and is only 1.4 times its probable error. So far as r can measure, no correlation exists between these characters. The correlation ratio $= 0.2993 \pm 0.0381$ and is 7.9 times its probable error. This constant, together with the rather high figure determined for Blakeman's test for linearity (B. T. = 3.5096), suggests the possibility of a correlation which r is unable to measure.

Table 15.—*Correlation coefficients (r) and their respective probable errors for each of the four homozygous awn-class groups of F_3 progenies*

[Grown in 1927 at Logan, Utah]

Characters correlated	r±P. E.	r/P. E.	Characters correlated	r±P. E.	r/P. E.
Awn class 4:			Awn class 3—Contd.		
Culm length × spike density	+0. 4857±0. 1074	4. 5	Awn length × neck thickness	+0. 1462±0. 1348	1. 1
Culm length × awn length	+. 7226± . 0672	10. 8	Awn class 2:		
Culm length × neck thickness	+. 4737± . 109	4. 3	Culm length × spike density	+. 2750± . 1300	2. 1
Spike density × awn length	+. 7857± . 0538	14. 6	Culm length × awn length	−. 0075± . 1406	.05
Spike density × neck thickness	+. 5867± . 0922	6. 4	Culm length × neck thickness	−. 4676± . 1099	4. 3
Awn length × neck thickness	+. 5451± . 0989	5. 5	Spike density × awn length	+. 0382± . 1404	.3
Awn class 3:			Spike density × neck thickness	+. 4492± . 1122	4. 0
Culm length × spike density	+. 5584± . 0948	5. 9	Awn length × neck thickness	+. 1709± . 1365	1. 3
Culm length × awn length	+. 0232± . 1376	.2	Awn class 1:		
Culm length × neck thickness	−. 0315± . 1375	.2	Culm length × spike density	+. 7991± . 0488	16. 4
Spike density × awn length	+. 2162± . 1313	1. 6	Culm length × neck thickness	+. 6777± . 0729	9. 3
Spike density × neck thickness	+. 5697± . 0930	6. 1	Spike density × neck thickness	+. 5924± . 0876	6. 8

Table 15 gives correlations between various plant characters when the progenies are grouped into the true-breeding awn-class groups. The awn 4 group gives a high correlation coefficient ($r = +0.7226 \pm 0.0672$) between culm length and awn length, which is 10.8 times its

probable error. Awn 3 ($r = +0.0232 \pm 0.1376$) and awn 2 groups ($r = -0.0075 \pm 0.1406$) give very low correlation coefficients, which in both cases are considerably less than their probable errors.

The correlation which η suggested seems to be located in fully awned progenies but not in the progenies of the other awn classes.

Culm Length and Neck Thickness

The correlation coefficient obtained for these two factors was $+0.1974 \pm 0.0345$. The constant is 5.7 times its probable error. The correlation ratio obtained ($\eta = 0.2538 \pm 0.0335$) is 7.6 times its probable error. Blakeman's test was 2.2263.

The awn 4 group has a fairly high plus correlation coefficient $\left(r = +0.4737 \pm 0.109 \text{ and } \frac{r}{P.\ E.} = 4.3\right)$. The awn 3 group has a correlation coefficient lower than its probable error ($r = -0.0315 \pm 0.1375$).

The awn 2 group has a rather high minus correlation coefficient ($r = -0.4676 \pm 0.1099$), which is 4.3 times its probable error. Awn 1 group has a high plus correlation coefficient ($r = +0.6777 \pm 0.0729$). It is 9.3 times its probable error.

Two of the four awn groups, then, show significant plus correlations. One of the other two groups shows a high minus correlation coefficient and the other a small minus correlation. It is apparent that since the correlations in two of the four are rather high plus and two are minus they would tend so to counterbalance each other when r was calculated for the entire family that a small r would be obtained.

Culm Length × Number of Culms

The correlation coefficient obtained for these characters is very small ($r = +0.0521 \pm 0.0357$), and is only 1.5 times its probable error. The correlation ratio obtained ($\eta = 0.1824 \pm 0.0347$) is probably not very significant when viewed in connection with the small Blakeman's test obtained (B. T. = 2.4427).

Spike Density × Awn Length

For these characters the correlation coefficient obtained ($r = -0.1112 \pm 0.0413$) is small, and is only 2.7 times its probable error.

The correlation ratio ($\eta = 0.3496 \pm 0.0367$) is fairly good sized, and is 9.5 times its probable error. Blakeman's test (B. T. = 3.9641) is also fairly high. These two constants indicate a correlation which r fails to measure. The correlation coefficients between spike density and awn length in the four awn groups are:

Awn group 4, $r = +0.7857 \pm 0.0538$ and $\frac{r}{P.\ E.} = 14.6$

Awn group 3, $r = +0.2162 \pm 0.1313$ and $\frac{r}{P.\ E.} = 1.6$

Awn group 2, $r = +0.0382 \pm 0.1404$ and $\frac{r}{P.\ E.} = 0.3$

The correlation indicated by η seems to be located again, as was the correlation of culm length × awn length, in the fully awned group, and to be lacking in the other awn groups studied. It was in fully

awned progenies that strong linkage was obtained between spike density and awn length in the Sevier × Kanred cross (*6*).

The value of η in indicating correlations which r does not measure is again brought out, rather clearly, in this instance.

Spike Density × Neck Thickness

The correlation coefficient for these two characters is perhaps high enough to be significant $\left(r = +0.4490 \pm 0.0286 \text{ and } \frac{r}{P.\ E.} = 15.7\right)$. A still higher correlation ratio $\left(\eta = 0.5711 \pm 0.0241 \text{ and } \frac{\eta}{P.\ E.} = 23.7\right)$ and a high Blakeman's test (B. T. = 4.9302) both suggest that there may be considerable correlation which r fails to measure.

For these same two characters Federation gave a correlation coefficient (Table 12) of $+0.6373 \pm 0.0658$ and $\frac{r}{P.\ E.} = 9.69$. For III C–18, r was $+0.1877 \pm 0.1070$ and $\frac{r}{P.\ E.} = 1.75$. The laxer of the two parents gave a good plus correlation. The denser parent gave a plus correlation which is probably too small to be significant.

In order to study these characters more fully, correlation coefficients were calculated for them in each of the three spike-density groups (homozygous dense, heterozygous, and homozygous lax). The coefficients of correlation with their probable errors are given in Table 16.

Table 16.—*Correlation coefficients (r) and probable errors (P. E.) for spike density × neck thickness in each of the three spike-density groups of F_3 progenies*

[Grown in 1927 at Logan, Utah]

Spike-density group	r±P. E.	r/P. E.
Homozygous dense	+0.3917±0.0638	6.1
Heterozygous	+.2612±.0481	5.4
Homozygous lax	+.6915±.0347	19.2

The correlation coefficient for homozygous dense ($r = +0.3917 \pm 0.0638$) is 6.1 times its probable error. For the heterozygous ($r = +0.2612 \pm 0.0481$) the constant is 5.4 times its probable error. For homozygous lax ($r = 0.6915 \pm 0.0347$) the constant is 19.2 times its probable error. While these coefficients are all plus and all high enough to be significant, there is a wide difference between the lowest and the highest. For indicating such a spotted or curvilinear condition in a population, η seems to be valuable.

Plus correlation coefficients were obtained, then, for the entire family, for both parents, and for each of the three spike-density groups. All were high enough to be significant except the III C–18 constant. (Table 12.) Spike density and neck thickness are, then, positively correlated.

All the data indicate that the laxer the spike the thicker the neck, and the denser the spike the thinner the neck. Since this relationship occurs consistently with the entire family, with the parents

(although to a much less extent with III C–18, the denser parent), and with the four homozygous awn groups studied, the suggestion is that it may be a physiological relationship.

Spike Density and Number of Culms

These characters gave a small correlation coefficient $\left(r = +0.0967 \pm 0.0355 \text{ and } \frac{r}{P.\ E.} = 2.9\right)$. The correlation ratio was somewhat higher but not significantly so $\left(\eta = 0.1833 \pm 0.0346 \text{ and } \frac{r}{P.\ E.} = 5.3\right)$. Blakeman's test for linearity was 2.1760.

Awn Length × Neck Thickness

The correlation coefficient for these characters is -0.2874 ± 0.0384, which is 7.5 times its probable error. The correlation ratio is 0.4068 ± 0.0349. It is 11.7 times its probable error. Blakeman's test for linearity is 3.4438, and suggests a stronger correlation than r measured.

A study of the 4 awn group throws some light on this (Table 15). Awn group 4 has a good correlation coefficient ($r = +0.5451 \pm 0.0989$).

The correlation coefficient for the awn 3 group is $+0.1462 \pm 0.1348$, and for the awn 2 group $+0.1709 \pm 0.1365$. In this case as well as in others previously discussed, the correlations are much stronger in awn group 4 than in the other awn groups.

Awn Length × Number of Culms

The correlation coefficient for these characters is $+0.0343 \pm 0.0418$. The correlation ratio is 0.3107 ± 0.0378 and is 8.2 times its probable error, and Blakeman's test is 3.6926. These latter figures suggest that there might be a correlation not measured by r. If such a correlation existed it was not found.

Neck Thickness × Number of Culms

This correlation coefficient is $+0.0265 \pm 0.0358$. It is smaller than its probable error. The correlation ratio ($\eta = 0.1755 \pm 0.0347$) is 5.1 times its probable error. Blakeman's test is 2.4232.

SUMMARY

III C–18 (a hybrid strain from a Sevier × Dicklow cross) and Federation were crossed. A vigorous F_1 family was chosen to continue the F_2 generation. Grain from each F_2 plant was used to seed one F_3 progeny row. The rows were spaced 1 foot apart and the kernels in the row were spaced about 3 inches apart. Paired plantings of the two parents were made in the same manner and at the same time after each 10 progeny rows.

Each F_3 progeny row was considered to represent the genetic constitution of its F_2 parent plant. There were 354 F_3 progenies. Data were collected for the various plant characters studied by observation or by measurement, as follows: Color of glume, awn class, culm

length, spike density, awn length, neck thickness, and number of culms.

Color of glume was found to be inherited on the basis of a 1-factor difference. The numbers obtained were 82 bronze, 176 heterozygous, and 96 whites. These numbers closely approach a 1:2:1 ratio. $P=0.5782$.

Awn classes were found to be inherited on the basis of a 2-factor difference with independent segregation. The numbers expected on this hypothesis very closely fit the observed facts. $P=0.9270$ and indicates an extremely good fit.

Culm length of the F_3 progenies was correlated with their F_2 parents to the extent of $+0.4316\pm0.0291$, which indicates that segregation occurred. The culm-length range in the parental rows was covered by the F_3 progenies.

Spike-density inheritance was peculiar in its nature. Three spike-density groups were found in the F_3 progeny—(1) homozygous dense, (2) heterozygous, and (3) homozygous lax with the respective numbers for each group of 81, 170, and 103. These numbers suggest a 1:2:1 ratio, with the goodness of fit as indicated by $P=0.1942$. The homozygous-dense progenies transgress the range of the dense parent in mean spike density. The dense parent III C–18 is possibly not recovered in a single progeny, and certainly not in more than two. The homozygous-dense progenies with these two possible exceptions are all more dense than the most dense of the III C–18. The group of heterozygous progenies fall between the two homozygous groups of progenies with no overlapping. (Fig. 7.) The range of densities of the heterozygous progenies cover that of the denser parent entirely. There is probably a 1-factor difference with perhaps some minor factors involved in the spike-density inheritance of this cross.

The awn-length range of the parental rows was recovered in the F_3 progenies. Homozygous awn group 1 was essentially the same as Federation in awn length. Homozygous awn 4 group recovered the greatest parental awn length. The other awn classes were graduated in length in rather regular order between awns 1 and awns 4. Standard deviations and coefficients of variability were distinctly higher for the segregating awn class genotypes than for the homozygous awn classes.

Neck thickness was essentially the same for the two groups of parent rows. The range in the progenies was small.

The number of culms was essentially the same in both parents and F_2 progenies.

Awn-class and spike-density characters were studied together to determine whether or not linkage existed. The 354 F_3 progenies were arranged into 27 genotype groups, which might be expected on the hypothesis of independent segregation with a 3-factor difference (two for awn classes and one for spike density). Their numbers approached the expected numbers. When goodness of fit was calculated, $P=0.4373$. This indicates that there is probably no linkage between spike-density and awn-class factors in this cross.

Correlation coefficients (r) and correlation ratio (η) and Blakeman's tests were calculated for various combinations of the following plant characters: Culm length, spike density, awn length, neck thickness, and number of culms.

Culm length seems not to be correlated with spike density in either of the parents, or in either of the three spike-density groups—homozygous dense, heterozygous, and homozygous lax. However, when the correlation coefficient was calculated for the entire family of the F_3 progenies there was a significant correlation, that is, the factors for the spike-density classes seem to have a distinct influence on culm length.

Culm length and awn length are distinctly correlated in the homozygous fully awned progenies. The other homozygous awn-class groups show no correlation. The entire family shows no correlation, yet $\eta(\eta = 0.2993 \pm 0.0381$ and $\frac{\eta}{P.\ E.} = 9.2)$ and Blakeman's test (B. T. = 3.5096) indicated the presence of a correlation, which was found in the fully awned group.

Spike density and awn length also seem to be correlated in the homozygous awn 4 group but not elsewhere. This correlation had also been indicated by the correlation ratio (η).

Spike density and neck thickness were found to be correlated in the Federation parent, in the four homozygous awn groups studied, and in the entire family.

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U. S. GOVERNMENT PRINTING OFFICE: 1929